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ARTICLE V.

THE SAPROLEGNACEÆ OF THE UNITED STATES, WITH NOTES ON OTHER SPECIES.

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Read before the American Philosophical Society, November 18, 1892.

In spite of the attention which most families of Thallophytes have received in the United States during recent years, the aquatic fungi have been hardly noticed. Although their resemblances to the Algæ on one hand, and to the Fungi on the other, give to their study peculiar interest, it is perhaps to this twofold affinity that the neglect is due. Their habitat is not such as is explored by the student of fungi, and the phycologist passes them by as not of his group.

The following pages contain the results of studies of American *Saprolegniaceæ*, carried on during the past two years in the intervals of other botanical work. The materials on which they are based have been largely procured by myself in and about Amherst, Mass.; but I have to thank the kindness of friends and correspondents in other parts of the country for considerable material illustrative of the Saprolegniaceous flora of their respective sections. Of these, I am indebted to Dr. Ida A. Keller, of Bryn Mawr College, for cultures from the neighborhood of Philadelphia, and for a single one from Kentucky; to Rev. A. B. Langlois, of St. Martinville, Louisiana, for cultures from that vicinity; to Prof. G. F. Atkinson, formerly of Auburn, Alabama, and to Mr. J. M. White, of Agricultural College, Mississippi, for specimens from those localities. I am also under especial obligations to Prof. William Trelease, of the Missouri Botanic Garden, at St. Louis, who has most generously placed in my hands without restriction all the preparations, notes and drawings made during his too brief study of the family, carried on chiefly in eastern Massachusetts

in 1881. I am also indebted to Prof. Roland Thaxter, of Harvard University, for specimens from Mt. Washington; and I owe to Mr. A. B. Seymour, of Harvard University, references to the few published *exsiccata* of this family and the examination of one of them. The others I have not been able to examine.

While neither the amount of material examined, nor the variety of sources from which it has been drawn, can justify any generalizations, they yet afford a basis for some preliminary ideas concerning the distribution and relative abundance of some of our species. The material has also been utilized, in part, for the study of several questions relating to the morphology of the group, on which it is hoped to shed some light. Physiological questions have not received the attention which they deserve, and which it is hoped to give them in future studies. Their discussion is, therefore, restricted as much as possible in the present paper, which is concerned chiefly with the morphological and systematic aspects of the family.

A pretty careful review of the literature has led to some conclusions concerning the synonymy of certain species not yet known to be American which have not previously been suggested. Therefore, it has been thought worth while to include in the systematic account of the family all published names, with an indication of the standing of each, so far as it can be determined from available data.

The appended bibliography makes no pretensions to completeness, but it is believed to contain the titles of all works of present value, or of much historical interest, relating to the morphology and classification of the *Saprolegniaceæ*, as well as those of certain other papers which are quoted in the following pages. Papers by American authors are marked with a dagger (†). The titles of the few papers included which I have not been able to examine are preceded by an asterisk (*). For access to many of the remainder I am indebted to the various libraries in Amherst, Boston and Cambridge, and to Prof. W. G. Farlow, of Harvard University. Each of the works is cited in the body of the paper by its abbreviated date, which is prefixed to its full title in the list. This method has the advantage of doing away with cumbersome footnotes, and of giving, in the briefest possible form, the date of the work with the reference to it. The last point is one of much convenience and economy in the citation of synonymy.

INTRODUCTORY.

The greater simplicity or apparent primitiveness of structure which is usually associated, among the simplest plants, with life in the water, together with the fact that various theoretical considerations point to the water as the probable habitat of the earliest forms of life, lends to the study of the aquatic Thallophytes the highest interest. Leaving out of consideration the natural and fairly circumscribed group of the *Schizophyta*, the great body of these forms is made up of plants containing chlorophyll, belonging to the algal stock, and presenting various lines of relationship and descent. From this stock must undoubtedly have been derived the great collateral chlorophyll-less groups of fungi. Most of the latter have been so modified to meet the conditions of aerial life, that the absence of chlorophyll has become of minor importance as a distinguishing character. A few, however, which cling to the ancestral habitat have preserved so many of the essential algal features that it becomes difficult to separate them from the *Algæ* except on the basis of their acquired saprophytic or parasitic habit and consequent loss of chlorophyll.

All of the characteristically aquatic groups of fungi belong to the most primitive or alga-like division—the *Phycomycetes*—and they are all probably to be regarded as primitively aquatic. Several interesting cases of transition from aquatic to aerial life are, however, presented by species immediately related to some aquatic ones and referrible to natural groups which may, in general, be called aquatic. The aquatic *Phycomycetes* may be grouped under five heads, as follows :

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|-------------------------------|----------------------------|
| 1. <i>Chytridiaceæ</i> . | 4. <i>Saprolegniaceæ</i> . |
| 2. <i>Ancylistaceæ</i> . | 5. <i>Pythium</i> . |
| 3. <i>Monoblepharidaceæ</i> . | |

The *Chytridiaceæ* constitute a heterogeneous group of considerable size and of much variety of structure. Its members are regarded by some writers as the most primitive of the fungi, and by others as degenerate forms derived from the higher *Phycomycetes*. They possess a very rudimentary mycelium or none at all, and commonly produce both sporangia, with zoöspores, and resting spores. An evident conjugation precedes the formation of resting spores in a very few cases; but, for the most part, the group presents no traces of sexuality. A considerable number of the species are parasitic upon terrestrial Phanerogams, usually such as grow in wet places; but the aquatic species constitute the larger part of the group and are also chiefly parasites. Their hosts include *Protozoa*, *Anguillulæ* and *Rotifera*; *Saprolegniaceæ*, *Algæ* of every group, various spores and pollen

grains; in short, a large part of the minuter organisms of fresh waters, to which they are chiefly restricted. A few species, however, are marine.

The *Ancylistaceæ* include a few species, chiefly parasitic upon *Conjugatæ* and *Anguillulæ*. The young plant is mycelium-like, but is entirely consumed in the formation of the reproductive organs. These are sporangia, oogonia, and antheridia. From the union of the protoplasm of the last two, there results in each case a single oöspore. While clearly related in their vegetative structure and habits with the *Chytridiaceæ*, these plants may be regarded as forming, in their reproductive organs, a transition to the higher *Oömycetes*.

The *Saprolegniaceæ* are to be discussed later.

Closely related to them, but differing in essential particulars, is the single genus *Monoblepharis* which forms the type of a distinct family. It has been studied only by Cornu, who has described three species. According to this author, the plants have sporangia with unciliate zoöspores; and the oöospheres, formed singly in the oogonia, are fertilized by motile unciliate antherozoids, produced in a cell cut off just below the oogonium from its supporting filament, which gains access to the oöosphere through an opening at the apex of the oogonium. These plants are saprophytes.

The *Peronosporaceæ* are represented among aquatic fungi by some of the members of a single genus, *Pythium*. Like the rest of the family, the members of this genus have an abundant mycelium from which are developed the sexual organs, antheridia and oogonia. Each of the latter produces a single oöosphere from a portion of its protoplasm, the rest remaining as "periplasm," and ultimately forming an outer coat about the spore. There appears to be an actual passage of protoplasmic substance from the antheridium to the oöosphere, constituting a real act of fertilization. In *Pythium*, as in some of the *Ancylistaceæ*, the zoöspores are formed outside of the mouth of the sporangium from the contents of the latter, after it has been extruded in a single mass. The aquatic species of the genus are parasitic on water plants or saprophytic on organic remains. One or more species attack terrestrial Phanerogams.

The American literature of these various groups is confined to a few scattered notes in addition to that quoted in the present paper, with the exception of Prof. Farlow's account of the genus *Synchytrium* of the *Chytridiaceæ*. Its members are, however, not aquatic.

This brief preliminary account may suffice to indicate the near relationship of all the aquatic fungi and to suggest the great morphological interest which attaches to them; while it may suitably preface the detailed discussion of the family which forms the subject of the present contribution.

SAPROLEGNIACEÆ.

The vegetative organs of these plants consist of usually branched tubular filaments without dividing walls, and therefore with a single continuous cavity. The filaments are of two sorts—the internal threads, which penetrate the substratum, branching freely, and tapering rapidly to their pointed ends (Fig. 2), and the external ones, which arise from the latter and radiate outward into the surrounding medium (Fig. 1). The following description refers chiefly to the latter.

In general, there are no sudden changes in the calibre of a filament, but only a gradual decrease from one end to the other; but the *Leptomitæ* are characterized by abrupt constrictions at intervals, marking off the hyphæ into segments, but not completely closing the cavity (Fig. 6). The hyphæ are usually largest at their bases; that is, where they arise from or give rise to threads of the other kind. From this point the external threads decrease slowly in size. Those of *Leptomitus*, however, decrease abruptly with each successive branching, so that their apical segments become reduced to an eighth of the diameter of the basal ones. The different species present very wide extremes in the size of their filaments, whose diameter may vary from 5μ in *Aphanomyces* to more than 100μ in *S. Treleaseana*. The length of the filaments in any given species or individual is considerably affected by the amount of available nourishment; but in vigorous specimens of *Aphanomyces* it may not exceed two or three millimeters, while in some *Achlyæ* it may reach more than twenty millimeters.

The hyphal walls of the members of this family are composed, unlike those of almost all other fungi, of unmodified cellulose, which reacts readily and characteristically with chloriodide of zinc. Within this wall is a layer of protoplasm which lines it closely and forms a hollow cylinder. At the centre is a wide vacuolar space, across which run, especially in the younger parts of the filament, strings of protoplasm connecting opposite parts of the parietal layer. This layer is densest and most granular in the youngest or apical part of the filament, and in the older parts the granular protoplasm forms a network of anastomosing threads or bands, with somewhat wide interstices (Fig. 4). In the threads of this network a constant circulation is kept up, towards the base in some and towards the apex of the hypha in others. It is worthy of remark that when young threads are cut off in water their death does not necessarily result. Very little protoplasm is lost from the tube thus opened, but a new cellulose wall is very quickly formed across the cut end (Fig. 3), and the hypha remains capable of normal development if nourishment be again sup-

plied, or even of developing until its protoplasm is exhausted, without further nourishment.

Scattered through the protoplasm without order, but commonest at the nodes of the granular network, are the nuclei, normally ellipsoidal in form, and each with a distinct central mass which stains more deeply than the rest of the nucleus (Fig. 4). These central masses have been generally termed nucleoli, but they seem clearly to correspond rather with the chromatin bodies of more highly organized nuclei, and will, therefore, be better designated as chromatin-masses. Between the chromatin-mass and the nuclear membrane is a considerable space occupied by a substance which stains very slightly with hæmatoxylin. The nuclei are most abundant in the young parts of the hypha, where the protoplasm is densest. They increase in number, with the apical growth of the thread, by fission. The division of the nucleus is preceded by the division of the chromatin-mass, and commonly occurs in a plane at right angles to its long axis (Fig. 5). I have observed some cases, like one shown in Fig. 4, where two nuclei lie close together, with their long axes parallel, but have never seen preliminary stages to convince me that they have resulted from the division of a nucleus in the plane of its long axis. Hartog states ('89) that he has observed karyokinetic phenomena in some cases, but I have been unable to find evidence of any other than direct division.

The growth of the hyphæ takes place at their blunt or somewhat pointed tips. Data as to the rate of growth are very few. Pringsheim ('51) reports a rate of 400μ ($= .4$ mm.) per hour in a new filament of *Saprolegnia*, growing into an emptied sporangium. Hine ('78) records having observed a growth of 70 to 90μ per hour during three hours' observation of a filament of *Saprolegnia*; and I have measured a growth of about 100μ per hour in a vigorous hypha of *Aphanomyces*, while the germ-tube from a zoöspore of the same species grew at the rate of about 40μ per hour in water.

The purely vegetative branching of the hyphæ is sometimes dichotomous at the principal divisions of the larger ones, but commonly of the monopodial type in the small branches. In most species the branches may arise from any point and develop by apical growth at acute or right angles with the main axis. In the genus *Leptomitus*, as here limited, branches arise only from the acroscopic ends of the segments, close to the origins of the next segments of the axial series (Fig. 6). They are separated by constrictions from their parent segments; but when the segment next below a sporangium gives rise to a branch, it grows out for a short distance without constriction, and then produces a new segment (Fig. 116), as Pringsheim has pointed out ('60).

The internal hyphæ, whose office is the absorption of nourishment from the substratum, may properly be termed *rhizoids*, whether from a morphological or a physiological point of view. DeBary states ('81, p. 95) that the external hyphæ may send down rhizoidal branches which penetrate the substratum. Well-developed threads, when cut off from their basal portions and brought in contact with fresh nourishment, will attach themselves to it by new rhizoids and continue their growth.

In addition to the protoplasmic contents and the food material diffused through it, the hyphæ of the *Saprolegniaceæ* contain more or less generally certain bodies as yet unrecognized in other plants. They have been called by Pringsheim ('83 *b*), cellulose granules (Fig. 6, *c*). They occur in the filaments or in reproductive organs formed from them, as discoid or lobed bodies, those of the latter form arising by fusion of several disks. When young, they are homogeneous and rather strongly refractive; and when old they often become distinctly stratified. They are, perhaps, most abundant and conspicuous in *Leptomitius lacteus*, where they were early described by Pringsheim ('60) as nuclei. In this species they often become lodged in the constrictions of the hyphæ and may completely close the passage. Pringsheim has shown ('83 *b*), that the substance of these bodies is neither a proteid nor a carbohydrate, although it is in some respects related to cellulose and starch. He regarded them as waste products of metabolism rather than as reserve materials, since he saw no evidence of their solution or transformation. But Rothert has shown ('88) that they probably contribute to the formation of the separating wall of the sporangium, since they seem to disappear during that process. It may also be suggested that cut hyphæ may owe their power of promptly repairing injury to the presence of this material. Should this be shown to be the case, they may be regarded as a soluble form of cellulose available for use in forming and repairing cellulose walls.

NON-SEXUAL REPRODUCTION.

After they have become well grown, the external hyphæ begin to produce the organs of reproduction, which are of two sorts, sexual and non-sexual. We will consider these as they are developed in the order of time, examining first those of non-sexual or vegetative reproduction. Only a single organ of this sort is common to the entire family; namely, the *zoösporangium*. Within this organ are produced the agents of the rapid propagation of the species concerned, the *zoöspores*. The phenomena of the development and individualization of the zoöspores within the sporangium appear to be essentially the same in most of the genera, at least. But the manner of their release from the sporangium and their subsequent history

undergo various modifications so characteristic and so related to each other that they furnish the basis for the grouping of the species into a natural series of genera. We pass to a detailed examination of their production and fate.

The first account to give an approximately correct description of these phenomena was that of Hannover ('42), followed by that of Unger ('43). Subsequently Pringsheim ('51) and DeBary ('52) extended their observations, and the subject has been a favorite one down to the present. The formation of a sporangium begins with the gradual cessation of the apical growth of a filament. Now commences an accumulation of protoplasm in the terminal portion of the filament, which usually becomes more or less swollen. No increase in size occurs, however, in the hyphæ of *Aphanomyces*. Finally the end of the hypha is filled with a very dense mass of protoplasm with numerous nuclei, which passes rather abruptly into the thin protoplasm of the lower part. In the narrow intermediate region between the dense and the thin protoplasm, is formed a clear disk of hyaloplasm, seen as a band in lateral view. Its hyaline character is due to the withdrawal of the microsomes from the originally granular protoplasm of that region. Across the lower surface of this disk is developed a cellulose wall, beginning at the wall of the hypha as a ring and progressing rapidly inward from all sides until the central opening is closed, and a solid wall separates the terminal portion of the thread, as a sporangium, from the remainder. It has been said that this basal wall of the sporangium is different chemically from the other cell walls of the plant. Not only is this improbable *a priori*, especially in view of its common fate in *Saprolegnia*, but careful examination shows that it reacts like the other walls with chloroiodide of zinc. As before remarked, Rothert ('88) has observed the occurrence of abundant cellulose granules in the region of the forming wall. Later these cannot be recognized and he suggests that they may furnish material for the wall. The hyaloplasm which thus at first lines the sporangial surface of this wall soon becomes again granular by the return of its microsomes.

The sporangium thus formed was regarded by earlier writers—Naegeli ('47) and others—as a free cell enclosed in the end of the filament. It differs widely in form in the different species, and even considerably in the same species. Commonly it is approximately cylindrical, and may be swollen most at its apical end (*Saprolegnia*), or in the middle (*Achlya*), with a length from six to twelve times its greatest diameter. In *Pythiopsis*, *Thraustotheca* and *Apodachlya pyrifera*, the length is so reduced that it becomes short-clavate or pyriform; and in some sporangia of *Pythiopsis* and in *Apodachlya brachynema*, the form is quite globular. These contracted forms occur also among more typical ones in *S. torulosa*. On the other hand,

the sporangia of *Aphanomyces* often reach a length of more than a hundred times their diameter.

In rare cases, the quantity of protoplasm contained in the sporangium may be sufficient to completely fill it, but usually it forms a parietal layer of greater or less thickness, with a vacuolar space extending through the middle. If this layer be very thin, or if the sporangium be completely filled, that condition will induce certain modifications in the usual course of development of the zoöspores, but in a great majority of cases the process is as follows. In consequence of the greater turgidity of the sporangium than of the lower part of its hypha, its basal wall becomes convex towards the base of the filament (Fig. 7, *a*). The first indications of the formation of zoöspores then soon follow. The phenomena attending this process have been the subject of much study and of widely different interpretations, most of which cannot profitably be detailed here. The most important contributions to the discussion have been those by Strasburger ('80), Büsgen ('82), Ward ('83), Berthold ('86), Hartog ('87), and Rothert ('88); and their papers may be consulted for the details of the various views put forth. Repeated studies of several species have satisfied me that Rothert's account, which is corroborated in most details by Berthold and Hartog, is practically correct. Therefore the following account is a combination of the descriptions given by those writers with personal observations. The description may best be based, as has been said, on the commonest form of sporangium, that with a parietal layer of protoplasm of considerable thickness and an axial vacuole. At first, irregular rifts begin to appear in the protoplasm, extending outward from the vacuole. They soon become more definite and more numerous, and connect with each other in such fashion that the protoplasm is marked off into a number of irregularly polygonal masses, as seen from the surface (Fig. 7, *a*). It is probable that the number of these blocks, which finally become spores, corresponds to the number of nuclei originally shut in by the basal wall, since the zoöspores are always uninucleate, and there is no evidence that any nuclear division occurs within the sporangium. The clefts are at first quite narrow, and the protoplasmic masses, or "spore origins," as they have been called, are frequently connected by threads of protoplasm. The somewhat irregular outlines and the granular structure of the origins, together with the appearance of the connecting threads in surface view, have led Strasburger, Büsgen and Ward to very different interpretations of these clefts from those here adopted. They have regarded them as "cell-plates," separating the spores, and consisting of layers—lines in optical section—of granules. But it is

clear that Rothert's explanation is the correct one, since, as the clefts broaden, the granules disappear, or separate with the origins.

At about the same time, with the appearance of the first signs of the segregation of the spore origins, there is formed, if the sporangium belong to a species of *Achlya* or *Saprolegnia*, normally at its apex, an outgrowth or papilla, from whose tip the zoöspores will finally escape. Its formation begins with the accumulation at that point of a mass of hyaloplasm which presses the wall outward. After its formation, the hyaloplasm becomes granular, except a thin layer which remains intimately connected with the apex of the papilla (Fig. 7, *a*). This apical wall is always less sharply defined and more highly refractive than any other part of the sporangial wall, and these characteristics become more and more prominent until the escape of the spores.

The clefts between the spore origins rapidly widen and deepen, causing the connecting threads to become broken and withdrawn into the bodies of the origins. In view of subsequent changes, and of what seems the most reasonable explanation of them, it does not appear probable that the clefts extend at once completely to the outer wall, although it is often very difficult or even impossible to detect with high powers and excellent material any protoplasmic lining of the wall at this stage, when the spore origins are most widely separated. Another good reason for believing that the origins are still connected by a delicate parietal lining may be found in the fact that the whole surface of an origin next to the wall remains closely applied to it throughout this stage, and does not become rounded off at the corners, as happens on the other sides of the origin, and on this side at a later stage.

After the separation of the spore origins has become nearly complete, there follows suddenly and without warning the so-called "homogeneous" stage of Büsgen, the "stage of swelling of the spores" of Rothert. The spaces between the spore origins disappear by the apparent swelling up and fusion of the separate origins, and the contents of the sporangium appear less opaque and less granular than before. In spots corresponding approximately to the middles of the spore origins are to be seen clear, bright spots, and throughout the whole protoplasm are numerous vacuoles which appear and disappear, shifting about rapidly (Fig. 7, *b*). At the same time with the beginning of this stage, there is a very sudden decrease of turgidity in the sporangium, which is shown by the flattening of the terminal wall of the apical papilla, previously convex outward, and by a complete change in position of the basal wall (Fig. 7, *b*). This wall has been until now, as before stated, convex downward, on account of the greater turgidity of the sporangium than of the lower part of its hypha. These relations evidently now become reversed, for the wall suddenly

becomes convex upward, indicating a marked and instantaneous loss of turgescence by the sporangium. All the characteristic phenomena of this stage are much more strongly marked in the species of *Achlya* (*A. Americana* and *racemosa*) than in those of *Saprolegnia* (*S. ferax* and sp. indet.) which I have studied. The change may come over a whole sporangium simultaneously, so far as the eye can detect, or it may begin at either end and extend, wavelike, to the other in two or three seconds. While the spore origins seem ordinarily to be quite fused together, careful examination will not seldom show, here and there in the protoplasm, narrow cracks which are the remnants of separating clefts not quite completely closed by the swelling of the origins. Rothert's explanation of this phenomenon seems to accord well with the observed facts and with what we know of cell structure in general. He believes that, until the beginning of the stage of swelling, the sporangium wall is lined by a continuous protoplasmic layer, and therefore, as in living cells generally, there can be no transfer of liquids between the cavity of the sporangium and the surrounding water. The final extension of some of the dividing clefts between the origins to the wall breaks the continuity of this "primordial utricule," and there is an escape of fluid through the pervious wall and a consequent loss of turgidity. This fluid is distinctly attractive to some forms of Bacteria which may be present in the surrounding water and is, doubtless, the cell sap. Its loss is due, Rothert thinks, to the contraction of the walls which have been distended by their dense lining, but now become free to assume their natural positions. Measurements show a reduction in the volume of the sporangium amounting in some cases to as much as thirteen per cent. After this loss, water is probably taken up by endosmose, and the mixture of cell sap and water in the cavity of the sporangium is absorbed by the spore origins, whose bulk is so increased that the separating spaces are practically obliterated. The successive absorption and expulsion of this fluid gives rise to the shifting vacuoles. My observation that sometimes in *S. ferax* the swelling of the spore origins begins perceptibly later than the incurving of the basal wall, distinctly corroborates this view.

A very few minutes after the swelling up of the origins, the vacuoles disappear, and the granular appearance returns. They begin again to contract, separating from each other on the old lines, as consecutive observation always shows. The contraction goes on rather rapidly, and the masses become definitely separated as independent spores. While this contraction is going on, small portions of protoplasm may become cut off from the different spores; but each is soon taken up, as a rule, by the same spore to which it originally belonged. The significance of this phenomenon will be discussed in connection with the sexual spores, during whose formation it also occurs. The gaps between the spores are widened by their contrac-

tion and the rounding of all their corners so that they come to lie nearly or quite free from one another. In *Achlya racemosa*, and perhaps in some other species, the contraction is much less pronounced than is usual, and its spores do not commonly appear distinctly separate in the sporangium.

Up to this point our account may apply equally to all the species that have been carefully studied. But we must now distinguish between those genera whose spores normally escape from the apex of the sporangium and those of which this is not true. In those of the former class (*Achlya*, *Saprolegnia*, and allied genera), there may often be seen some spontaneous movement among the spores, especially among those near the tip. In case of the two genera just named, the apical papilla becomes markedly more transparent and less sharply outlined, as to its terminal wall. As the spores acquire more exactly their ultimate form, the motion increases and the terminal wall fades out until it is ruptured, and the spores rush through the opening (Fig. 8). Sometimes the wall seems to soften gradually until it yields to pressure from within; or again, the spore nearest the apex may be seen to enter the papilla and apparently to force its way through the partly softened wall, thus making an opening through which the rest rapidly follow. Other modes by which the opening is made have been detailed by Rothert ('88), but need not be further discussed here.

Some figures concerning the rapidity of the development of the zoöspores have been given by others, and I have made notes of the process in the four species chiefly studied. Ward ('83) gives some observations on *A. De Baryana* ("polyandra") and *A. apiculata*, and these accord with my own on *A. Americana* and *racemosa* as closely as could be expected. There is considerable variation in the time occupied, depending on the age and vigor of the culture, and doubtless on various undetermined conditions. A general statement may, however, be based on the data at hand. The first appearance of the clefts, which mark the beginning of the formation of the zoöspores, usually occurs twenty or thirty minutes after formation of the basal wall. From their appearance to the escape of the zoöspores the time may be from twenty-five minutes to an hour, but it rarely exceeds forty-five minutes. The emptying of the sporangium is ordinarily accomplished in from forty-five to one hundred seconds.

The zoöspores are ovate or pyriform, and their protoplasm is hyaline at the smaller end, while in the rest of the spore it is very granular, and contains two or three contractile vacuoles (Fig. 8, z, and 9). The zoöspores of the species of *Saprolegnia* (Fig. 8, z) and *Pythiopsis* (Fig. 63, z), and of some, probably of all, species of *Achlya* (Fig. 9) are provided with two cilia attached to the smaller, hyaline end of each. The presence of these organs in the first-named genus has been recognized since they were demonstrated by Thuret ('50), but Cornu was the first ('72) to assert

their presence in *Achlya*. Hartog ('87) later corroborated his statement for *A. polyandra* and *recurva*. I have several times recognized cilia on the zoöspores of *A. Americana*, at the instant of escape, by adding to the water on the slide supporting the specimen a few drops of a one per cent. solution of osmic acid in water, and then staining *in situ* with a solution of equal parts fuchsin and methyl violet in strong alcohol. This treatment, recommended by me ('91) in a previous note on the subject, demonstrates the presence of cilia unmistakably. In an exceptionally favorable specimen of *A. Americana* I have seen the cilia on the living zoöspores, both before and after their escape from the sporangium; and in *A. polyandra* one can hardly fail to notice the very marked ciliary motion within the sporangium during the escape of the spores. It is not improbable that the zoöspores of *Aphanomyces* are also ciliate, but this has not been shown, and the genus needs more careful study than it has yet received.

Sometimes the spores escape with the ciliate end directed forward, but it appears to be much more usual for them to pass out in the reverse position. The first spores to leave do so very rapidly, and are closely crowded together, as though strongly impelled from behind or attracted from before. In the species of *Achlya* all the spores press outward in a close column, but in *Saprolegnia* there is a gradual decrease in the rapidity of their escape, and the last spores may linger for some seconds or even minutes, swimming aimlessly about, and sometimes never finding the exit.

The zoöspores of *Saprolegnia*, *Leptolegnia*, *Pythiopsis* and *Leptomitus* escape separately into the water, and swim about freely by means of their forward-pointed cilia. After a short time, varying from a few seconds to fifteen minutes, each spore ceases to move about, but continues for a time longer to whirl and rotate, assuming meanwhile a spherical form. Sometimes a few whirls are followed by complete quiet, but often the spore continues to struggle for ten minutes or more, as if in vigorous protest against giving up its activity.* Finally, it becomes quite spherical and motionless, though the cilia may occasionally be seen to wave slowly for a time longer, and then to disappear by degrees, being apparently withdrawn into the protoplasmic mass. The spore now becomes encysted by the secretion of a cellulose wall, and so, for the first time, constitutes a closed cell. Huxley has stated ('82) that the spores

* A curious phenomenon, calculated to arouse speculation as to the nature of the changes of relations and tensions which take place while the zoöspore is coming to rest, has been observed by me in a spore of an undetermined *Saprolegnia*. After swarming normally, the spore had nearly come to rest, though with prolonged and vigorous struggles, when suddenly it burst with much force, scattering most of the granular protoplasm to a considerable distance, and leaving where it had been the nucleus with a small part of the protoplasm. There was, as yet, no trace of a membrane.

of the *Saprolegnia* of the salmon disease become motionless and encyst without swarming on leaving the sporangium.

The zoöspores of *Achlya*, *Aphanomyces* and *Apodachlya* only reach the water just outside of the sporangium, and there become encysted, each one, as it leaves the mouth, slipping into its place and rounding off at once, so that all the spores from a sporangium form a hollow sphere or hemisphere, into which the tip of the sporangium projects slightly (Figs. 10, 11). In other words, their cilia serve to carry the spores only through the mouth of the sporangium. In *Achlya* the escaping spores form a column so compact that considerable space is left between it and the wall, and they cling closely together during the entire emptying of the sporangium. It is always noticeable that the spores in this column keep their long axes parallel with each other. In *Aphanomyces*, each of whose sporangia produces but a single file of zoöspores, the spores are compelled by the narrow space in which they are formed to take a cylindrical shape. They pass in slow succession down to the mouth, and there become encysted (Fig. 11). There is no crowding or clinging together, and the complete emptying of the sporangium requires a much longer time than in the genera already described.

Hartog attributes this encystment of the spores at the mouth of the sporangium to a mutual attraction between them which he terms *adelphotaxy*, and which is also shown in their pressing closely together during their escape, in *Achlya*. It may well be that in *Aphanomyces* they are prevented by their narrow quarters from showing the same peculiarity inside of the sporangium. If we accept the existence of such an attraction, we must believe that it is stronger than the power of the cilia to carry the spores apart, or else that it is concomitant with a very transient development of cilia. In the present state of our knowledge some assumption is necessary to account for the phenomena which have been described. The spores are held together by no material connections, and, at least in some species, are provided with cilia. That these phenomena are dependent upon the life of the spore is shown by the fact that, if a solution of osmic acid, which instantly kills and fixes the spores, be added at the moment of escape, not only is their accumulation into a sphere stopped, but they are freely separated and carried about by diffusion currents in the surrounding liquid. It is hardly necessary to add that osmic acid would so harden any accompanying mucus from the sporangium that the spores would be held firmly fixed if such substance were present, as some writers have believed. Hartog's assumption of a mutual attraction between the spores seems as little open to objection as any that can be suggested, and should be so stated as to include a tendency to place their long axes parallel. This tendency, combined with the effort to secure as much expo-

sure as possible to the surrounding medium, may account for their arranging themselves in a hollow sphere.

We may ask here what causes lead to the emptying of the sporangium. The existence of a special expulsive substance which swells strongly on absorbing water was assumed by earlier writers, Strasburger ('80), Büsgen ('82) and DeBary ('84). It was believed that the supposed "cell plates" of the first separation stage swell into an intermediate substance enclosing the spores and expelling them by its rapid and enormous increase in volume when water enters the sporangium. But the existence of this hypothetical substance has been sufficiently disproved along with that of the "cell plates." The only species in which an intermediate substance appears to exist is one in which it could be of no service in expelling the spores, as will be seen later; namely, *Thraustotheca clavata*. Since this species was the one which Büsgen studied in most detail, the reason for some of his views becomes evident. In general, there can be little doubt that the spores of the genera now under discussion leave the sporangia automatically. The preliminary changes in the wall, normally at the apex of the sporangium, which render the escape of the spores possible, involve interesting physiological questions which will not be discussed at present. But the nature of the stimulus which causes the spores to avail themselves as quickly as possible of the means of escape provided, may be briefly discussed. It frequently happens in *Achlya* and *Saprolegnia* that the spores do not leave a sporangium which has opened normally, but become encysted within its interior. This failure to leave the sporangium must evidently be due to the absence of the usual stimulus. Hartog ('87), and before him Cornu ('77), has held that the presence of free oxygen in the water is the determining factor. Rothert ('88) disputes this view, as well as Hartog's statement that such sporangia appear chiefly in poorly aerated cultures. And Hartog has more recently ('88) suggested that the spores may vacate the sporangium to find purer conditions than prevail within it; in other words, to escape from the products of their own metabolism.

In the first place, it may be remarked that it is much less probable that the hereditary phenomena of spore development within the sporangium should vary than that differences should occur in the external conditions of different cultures, or of the same culture at different times. Since there is no evidence that the formation of the spores presents any abnormality in those sporangia which fail to discharge their contents, we cannot suppose that the need of purer conditions exists less in one sporangium than in another. But some sporangia with normally developed mouths fail to discharge their spores when others are wholly emptied, though it is more common to find most of the sporangia formed at a given time in the same condition in this

respect. This points strongly to some attractive and variable constituent of the surrounding medium as the cause of the normal exit of the spores.* The aimless wandering and frequent failure to escape of the last few spores in a *Saprolegnia* sporangium may be attributed to the fact that the water from outside has so far filled the sporangium that the difference between the media within and without the sporangium has become practically neutralized by their mingling. That the attractive force is normally very strong is shown by the following observation. A sporangium of *Achlya Americana* had developed abnormally three escape papillæ, one near the apex, one near the basal wall, and one midway between the others, all on the same side. The middle mouth was the first to open, and the spores rushed out in normal fashion until about a third of them had escaped. Then the other two mouths opened almost simultaneously, and the spores nearest them broke away from the column of which they formed a part, and crowded out through the new openings. Thus the force causing their exit was stronger than their tendency to cling together, and drew those within its range away from the main body. Whether the attraction is due wholly to the presence of free oxygen seems still open to doubt, although Hartog's experiments ('88) show it to be a factor of prime importance. It is true that failures of the sporangia to empty normally occur often in old cultures in which the oxygen may well be largely exhausted, and very often in cultures which have become overrun by Bacteria, Infusoria, and other foreign organisms. But cases occur which do not seem explicable on this basis alone. For example, in cultures on the slide with a comparatively small quantity of water, though quite sufficient for the swarming of zoöspores, sporangia often fail to become emptied, yet here there can be no suspicion of any lack of oxygen, but rather an unusual abundance of it.

In spite of the great differences in the size of the sporangia in different species of *Saprolegniaceæ*, and even in the same species, the size of the zoöspores, as measured after their encystment, varies but little, except in *S. anisospora*, which is not yet known to be American. The encysted spores are quite exactly spherical in all the American species studied, and are almost always between 8 and 12 μ in diameter. Those of a given species may show a tendency toward one or the other of these extremes, but they present no constant characters in this respect, and are of absolutely no diagnostic value. Each spore contains a single nucleus, one of the original nuclei of the sporangium, of a nearly globular form, but otherwise like those of the

* On the other hand, the mouths of some *Saprolegnia* sporangia often resemble very exactly the opening formed in a glass tube with one closed end, by forcing air into the open end while a small area on the wall is softened in a flame. The likeness is so striking as to suggest at once the action of an impulsive force from within the sporangium (see Fig. 50).

growing filaments (Fig. 12). The number of spores formed in a sporangium depends, then, on its size and the thickness of its protoplasmic lining. In an undetermined species of *Saprolegnia* I have estimated as nearly as possible the number of zoöspores produced in each of two sporangia of different sizes, with protoplasm of about average thickness. One 270_{μ} long by 26_{μ} in average diameter gave rise to about 120 spores, while from one $373 \times 32_{\mu}$ about 250 spores escaped. A comparison shows that the volumes of these two sporangia bear almost precisely the same relation to each other as the numbers of zoöspores formed in them.

After remaining encysted for a few hours, the zoöspore begins to show renewed activity. A small, circular perforation is made in the enclosing wall, and the contents begin to emerge in the form of a small papilla, which gradually enlarges until finally the entire protoplasmic mass lies outside of the cast-off membrane (Fig. 11). The mass soon takes the form of a biciliate zoöspore, and after some preliminary efforts, darts away and swims freely about. In this second active stage the spore has exchanged its original form for that of a kidney bean, its cilia being attached at the lateral depression which corresponds to the hilum of the bean (Fig. 11, *z'*). At the point of attachment the protoplasm is, as in the first form, hyaline. The cilia are of unequal length, and the shorter is directed forward, the other backward, during the swarming. It is an interesting fact that this form of the zoöspore corresponds with those of the related *Peronosporaceæ*, and with those of some of the *Ancylistaceæ*. It would seem that this must be regarded as the primitive zoöspore of the *Phycomycetes*, as Ward has suggested ('83), the form with apical cilia being a secondary one acquired within the limits of the present family. After half an hour or more of activity, the spore again settles down and becomes encysted as before.

In most of the genera now under discussion, this double swarming or *diplanetism* of the zoöspores is the rule, although in exceptional spores the second swarming may be omitted without apparent influence upon their germinating power (Fig. 11, *a*). It would seem that the object of the first swarming is the emptying of the sporangium, and that of the second the distribution of the spores, to enable them to reach new sources of food supply; since, as Pfeffer ('84) has shown, they are strongly attracted by various organic substances. Although the first swarming accomplishes both ends to a considerable degree in *Saprolegnia*, it does not permit the wide distribution which the longer second period allows. The zoöspores of the second form also seem to range over a much wider region and to be more actively locomotive than those of the first. The condition which is exceptional in most of these genera has become permanent in *Pythiopsis*, which may represent a reduced *Saprolegnia*, that,

finding its first swarming period sufficient, has dispensed with the more primitive second one.

Pringsheim states ('60) that the zoöspores of *Leptomitus lacteus* germinate after a single period of activity. I have seen, however, in pure cultures of this form, abundant empty membranes with every appearance of having been cast off by a diplanetic zoöspore (Fig. 118); but unfortunately, I have not observed the actual escape of the spores from them.

After its final encystment the spore may germinate at once, if conditions are favorable; or may remain for a short time capable of germination. In germination the wall of the encysted spore grows out at one or more points into as many slender tubes (Fig. 11, *a-i*), which may reach a length equal to several times the diameter of the spore without nourishment. They soon exhaust the nourishment contained in the spore, and, if more be not supplied, cease growing and die. If, on the other hand, food is accessible, growth becomes more rapid and the tubes develop into vigorous hyphæ. At the very beginning of germination, the nearly spherical nucleus of the spore takes a more elongate form and divides into two (Fig. 13); and by the repeated bipartition of these nuclei and their descendants arise all the nuclei of the hyphæ derived from the spore.

Some observations on the rate of growth of a germ tube of *Aphanomyces* sp. may be worth recording here. The tube was produced by a spore which remained encysted in the head after all the rest had passed into the second swarming stage, and was growing, therefore, without access to food (Fig. 11, *a*). At ten A.M. the tube was just visible as a slight protuberance from the spore (Fig. 11, *a*); at eleven it had reached a length of 37μ (Fig. 11, *g*); and at twelve it was 52μ long (Fig. 11, *i*). The effect of the absence of a supply of food is plainly shown here. While the growth during the first hour under the stimulus of the reserve materials contained in the spore amounted to 35μ , that of the second hour, when this supply was becoming exhausted, fell to 15μ .

We pass now to a comparison of the genera *Thraustotheca*, *Dictyuchus* and *Aplanes* with those already described. It has been said that the zoöspores of *Saprolegnia* and *Achlya* sometimes become encysted within the sporangium. This condition is the normal one in the genera above named, but in these the development of a mouth at the apex is wholly suppressed. In *Thraustotheca* the entire wall of the sporangium, except a narrow basal ring, breaks up after the encystment of the spores and leaves them free or slightly held together by an intermediate substance. After a time, they swarm in the laterally biciliate form, encyst again, and germinate. The sporangial wall of *Dictyuchus*, on the contrary, does not break down, and the encysted

spores press each other so closely that they become irregularly polygonal. Finally they escape separately through circular perforations of the sporangial wall, just as the spores of *Achlya* escape from their cysts, and swarm in the usual second form. The close compression of the spores within the sporangium leads to a complete fusion of the encysting wall of each one with those of the others which it touches and with the sporangial wall. This must be, at least, the morphological explanation of the structure, although the membrane separating two spores may probably arise as a single one. After the escape of the spores, as above described, there is left in the sporangium a network of the apparently single walls which separated them (Fig. 112). Their escape, like that of an *Achlya* or *Saprolegnia* spore from its cyst, is a slow operation. The time from the beginning to the completion of the escape of the protoplasm of a single spore may be half an hour or even more, and several hours may be occupied in the complete emptying of the sporangium. The separate spores follow no order in their escape, but several in all parts of the sporangium may be escaping together (Fig. 16).

After its emergence the roughly globular mass contracts and becomes more elliptical, while cilia appear and slowly lengthen. At length, twenty or thirty minutes after escaping, in case of the undetermined species studied (Fig. 16), only four or six minutes after in *D. monosporus*, according to Leitgeb ('69), the spore darts away.

In *Aplanes*, according to De Bary ('88), both swarming stages are suppressed, and the spores, encysted within the sporangium, produce their germ tubes, which pierce its wall and so reach the water, and perhaps fresh nourishment. But it must be observed that their loss of the power of locomotion greatly diminishes the probability of this result. This lessened value of the sporangia as organs of propagation may explain in some measure the fact that they are rarely developed in this genus.

In *Saprolegnia* and *Achlya* those spores which encyst within the sporangium may escape and swarm in the second form, or they may germinate *in situ*. It is evident that the former condition corresponds to a sporangium of *Thraustotheca* with a permanent wall, or to one of *Dictyuchus* in which the spore cysts have remained separate, while the latter is just that which is normal for *Aplanes*. Abnormal sporangia of genera whose spores are normally diplanetic may therefore be designated as "dictyosporangia," or as "aplanosporangia," according to the degree of abnormality shown. Species of *Dictyuchus* may bear aplanosporangia.

After the emptying of the first sporangium formed from a filament, which may be termed a primary sporangium, a second one is very commonly developed from the same hypha, and after it often a tertiary one, and so on for a variable number of generations. The sporangia of the second and later generations arise by one of three

different modes, in a given species. In *Leptomitus*, they are formed in basipetal succession, each segment of the hypha becoming in its turn a sporangium (Figs. 115-117). In *Saprolegnia* and *Leptolegnia*, the new sporangium begins by the upward growth of the basal wall of the old one, which continues so that the new fills the cavity of the old more or less completely (Fig. 14). It may even grow out through the mouth of the latter for some distance. It is not uncommon to see several successive sporangia thus "nested" (Fig. 15). Rarely in most species of the genus, but often in *S. monilifera*, according to De Bary ('88), the renewal of sporangia by the third mode, now to be described, occurs. The genera *Pythiopsis*, *Achlya*, *Aphanomyces*, *Thraustotheca*, *Dictyuchus* and *Apodachlya* are characterized by the cymose branching of their hyphæ in the production of new sporangia. Just below the basal wall of the primary sporangium arises a lateral branch which, after a period of growth, develops a secondary sporangium at its tip. Successive repetitions of this sympodial branching on alternate sides of the apparent axis produce a scorpioid cyme, which is usually developed with more or less regularity (Fig. 10). In *Pythiopsis* there is a more pronounced tendency to the development of a one-sided or helicoid cyme (Fig. 62). Variations from perfect regularity are, however, the rule in most forms. It often happens that a branch remains short, and forms a single sporangium with a part of the axis (Fig. 10, 3). Less often a secondary sporangium is formed below the primary one, as in *Leptomitus*. In *Aplanes* the sporangia are so sparingly developed that the formation of secondary ones has not been observed. Hartog has stated ('88) that the sporangia of *Aphanomyces* are renewed as in *Saprolegnia*, but this is certainly not true for *A. scaber*, in which cymose branching occurs (Fig. 17); and the same condition probably exists throughout the genus.

The name *resting sporangia* has been applied to sporangium-like structures which, after being cut off from their filaments, remain unchanged for a time, but which may, under suitable conditions, develop and discharge their zoöspores in the usual way. They are evidently sporangia arrested in their development, probably by external conditions. Their simplest form is that of the ordinary sporangium, but frequently they are shorter and broader, and formed in series from the hyphæ.

Chlamydospores. Many of the species of *Saprolegniaceæ* may produce other structures beside the sporangia, that are organs of non-sexual propagation and may be termed chlamydospores, in the sense in which Brefeld uses that term. They are usually developed in series, as swellings at the ends of the hyphæ (Fig. 18), and

in their completest development are globular in form (Fig. 19), with dense protoplasm and slightly thickened walls. The connection between the members of a series becomes very slight, and they easily fall apart. They may germinate soon after their formation or after a longer time, but constitute essentially a resting state of the plant, as compared with sporangia. Their germination consists in the production of a germ tube or hypha, from which is formed a sporangium with zoöspores after a brief growth. This distinction should be emphasized, that whereas the zoöspores are formed *within* the "resting sporangia," the chlamydospores produce them in a distinct germ tube, although the interior of the chlamydospore is often included in the cavity of the sporangium (Fig. 20).

Schroeter ('69) has described the formation of "gonidia" in *Achlya*, but what he saw appear to have been rather "resting sporangia" than true chlamydospores. Walz ('70) observed and figured the latter in a species of *Saprolegnia*, and Brefeld describes ('81) similar structures. They occur also in *Aphanomyces* according to Sorokin ('76), and Zopf finds bodies of this nature to be constant and characteristic in *Apodachlya pyrifera*. But in the last case they are sometimes lateral in position, are never produced in chains, and appear to be the normal resting form of the plant. Well-developed organs of this sort have appeared in a culture of *Achlya Americana* (Fig. 18); and in one from a tank for tropical plants under glass they were abundantly produced by plants with the sporangia of *Achlya*, on which they completely replaced the usual sexual organs (Figs. 19, 20).

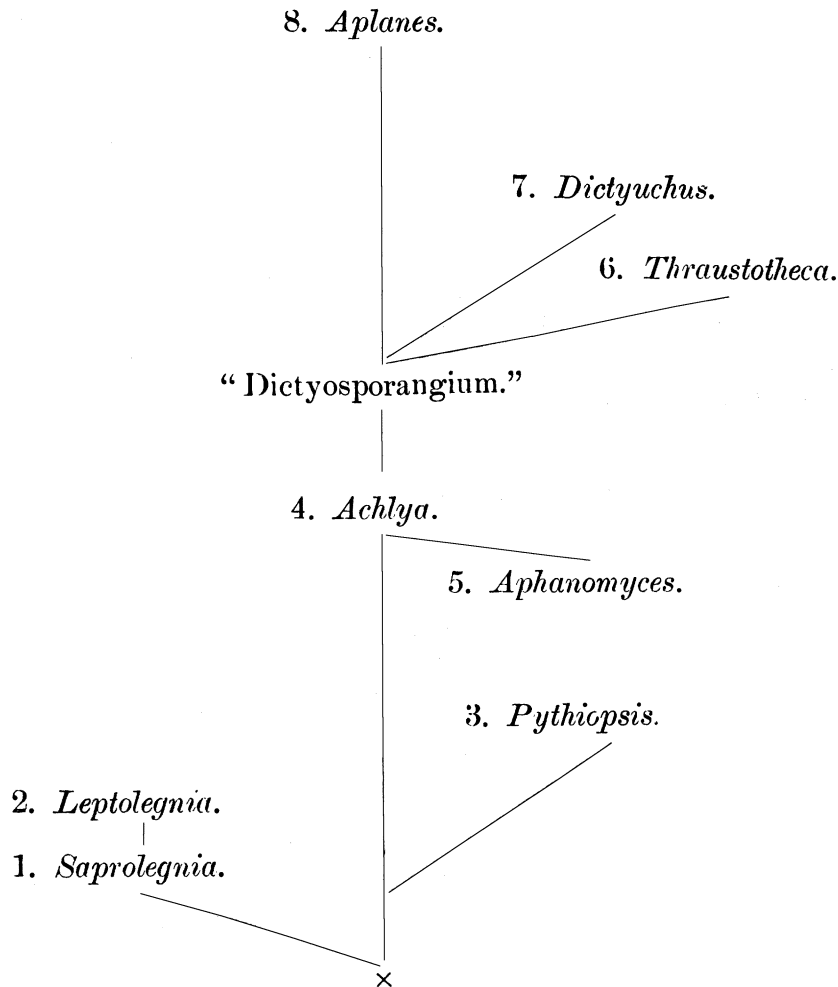
In comparing the organs of non-sexual reproduction in the *Saprolegniaceæ*, we observe that they do not differ in any essential feature of their origin and formation. They are, in other words, morphologically similar. But, while the office of the sporangia is the rapid propagation of the species, the chlamydospores have acquired the resting habit, and the *spore* character in the development of a germ hypha. The "resting sporangia," in their more specialized forms, constitute an evident link between normal sporangia and chlamydospores.

When considering the generic relationships within this family, and the best arrangement for indicating these relationships, one is forced to the conclusion that, notwithstanding the similarities in structure which have caused Pringsheim ('60) and Hartog ('87) to consider the differences of minor importance, yet the constrict-

tion of the hyphæ, the absence of sexual organs in most species, and their peculiarities in the single species in which they are known, with minor variations, of little weight individually, which distinguish the species of *Leptomitus* and *Apodachlya* from the others of the family, justify their separation as a distinct subfamily. The discovery of sexual organs in one of these plants, on the other hand, confirms the indication of the zoöspores that they should be included in the present family. Setting them aside, then, as *Leptomiteæ*, we may examine the genera constituting the *Saprolegnieæ*.

It is evident that the most primitive condition as regards the zoöspores is presented by the typically diplanetic form, as found in *Saprolegnia*. But the renewal of sporangia occurs most commonly, and apparently most typically, by lateral, cymose branching. Assuming as the primitive form an hypothetical one combining the two characters above indicated, we must place first in the series *Saprolegnia* and *Leptolegnia*, differing from it only in respect to the second point. *Pythiopsis* has economized by suppressing the second swarming stage, and stands alone on this line of development. In *Achlya* the first swarming has been reduced to a minimum by the mutual attraction of the spores, a newly acquired feature, and *Aphanomyces* seems best regarded as a degenerate *Achlya* rather than as a primitive one. In the remaining genera the reduction of the first swarming stage, begun in *Achlya*, is carried to complete suppression. The condition presented by a dictyosporangium of *Achlya* is in the direct line of development from the normal type of that genus, and that of the aplanosporangium is a further step on the same line. The former condition becomes modified in two ways—in *Thraustotheca*, by the early breaking up of the sporangial wall; and in *Dictyuchus*, by the coalescence of the encysting walls and the development of numerous secondary mouths instead of the original primary one. The latter condition becomes permanent and typical in *Aplanes*.

These ideas concerning the relationships of the genera may be graphically expressed as follows:



SEXUAL REPRODUCTION.

The reproductive organs of the second class are morphologically sexual, though, as will be seen later, they are not physiologically so in all cases. In the following account they will be described as sexual organs without reference to the occurrence of a definite sexual act, which will be subsequently discussed. Since they are the morphological equivalents of the truly sexual organs of related fungi, there is no occasion to change the names which they received when believed to be also their functional equivalents.

All of the described species of *Saprolegniae* produce sexual organs, usually after the maximum development of sporangia has been passed; indeed it is impossible to distinguish the species except by their sexual organs. None of the *Lepto-*

miteæ has been known heretofore to bear them, and their peculiarities in the single form in which these have been seen will be discussed in connection with the description of that species (*Apod. completa*). The special office of these organs is the production of bodies which, like the chlamydospores above described, may in some cases germinate at once, but ordinarily constitute a resting condition of the fungus. The conditions most favorable to the development of the sexual organs are not yet fully understood, and the readiness with which they are produced varies much with the species. The species of *Saprolegnia*, for instance, produce their sexual organs less freely and less certainly in cultures than do those of *Achlya*.

The sexual organs are produced, like the sporangia, from the main hyphæ or from branches, and are commonly terminal, though sometimes intercalary, in position. The female organ, the *oögonium*, develops as a swelling of the thread which bears it, which may be termed, when not a primary filament, the *oögonial branch*. The swelling increases as the protoplasm accumulates, until its definite form is reached. If the oögonium be terminal, its form is most commonly globular (Figs. 52, 71), though often with a cylindrical basal portion (Fig. 43), and sometimes ellipsoidal (Figs. 87, 99). When the extreme tip of the hypha is not involved in the swelling, it forms an apiculus to the oögonium (Figs. 27, 57). Intercalary oögonia are oftenest barrel-shaped (Fig. 59). After the form and size of the oögonium has been determined, it is separated from its hypha by a transverse wall, or, if it be intercalary, by two such walls. The formation of the walls is characterized by the same phenomena which are observed when the basal wall of the sporangium is formed. The wall of the oögonium has meanwhile been thickening by the deposit of new material upon its inner surface. In the simplest cases this deposit takes place evenly, producing a smooth wall of equal thickness throughout (Fig. 81). A somewhat less even deposit produces a roughened inner surface (Fig. 77); or the thickening may be wholly lacking on certain definite areas more or less numerous scattered over the wall of the oögonium, causing the pitting of the membrane which is a constant and characteristic feature of certain species (Figs. 43, 72). Instead of presenting a smooth outer surface, the whole membrane may be, from a very early stage, raised at intervals into outgrowths of varying height and frequency, giving it a warty or spiny appearance (Figs. 55, 104).

While the membranes of the vegetative filaments and of the sporangia always give the characteristic cellulose reaction with chloroiodide of zinc, those of the fully developed oögonia take with this reagent* a beautiful Indian-red shade, showing that

*This was prepared by dissolving Grüber's solid chloroiodide of zinc in its own weight of water, or somewhat less, and then adding metallic iodine until the desired sherry-brown color was obtained.

some chemical change has taken place. Since the pits are marked by colorless areas in the otherwise deeply colored wall, the original membrane must have become so changed, at those points at least, that it remains uncolored by the reagent. It seems probable that the whole outer membrane assumes this character, and that the color is produced entirely in the secondary deposit.

The male organs, or *antheridia*, are, when present, almost always borne on slender lateral *antheridial branches*. In some species they are very rarely or never developed (Figs. 43, 104). Where they are present, they are not necessarily found in connection with all the oögonia (Figs. 40, 75, 76), though they may be invariably so (Figs. 52, 71, 105). The number of antheridia attached to a single oögonium shows very little tendency to definiteness, except in *A. racemosa* (Fig. 94). The most that can be said is that in a given species there is a general tendency to an abundant production of antheridia, or the reverse.

The antheridial branches arise from the main filaments or from oögonial branches, sometimes exclusively from one or the other, in other species from both. They may be very short and simple (Fig. 98), or long and much branched (Figs. 51, 71). From their tips antheridia are cut off by transverse walls, and rarely are intercalary also. The antheridia are cylindrical or clavate in form, somewhat thicker than the branches, and with slightly denser protoplasm. Their form is very constant for a given species and, in connection with their position and origin, affords important characters for specific diagnoses. Their walls show in a less marked degree the reaction of the oögonial walls.

The same primary filament may give rise to both oögonial and antheridial branches, or it may produce only those of one sort. Since it is practically impossible to determine in ordinary cultures whether two filaments belong to the same plant, and since definite cultures from a single zoöspore have not been made, we cannot say whether species whose hyphæ are unisexual are truly diœcious or not. It is safe, however, to apply to them the term used by DeBary, *diclinous* (Figs. 51, 88). The same author calls species with bisexual filaments *androgynous*. Among species of the latter kind, which constitute the large majority of the *Saprolegniæ*, the antheridia may attach themselves to oögonia from the same or from other filaments. Most of them reach oögonia from the same hypha, probably because these are nearer.

In one species not yet met with in America, *S. hypogyna*, a single branch is bisexual, the antheridium being formed from a cell cut off by a second wall immediately below the oögonium. This is the only known case in this family of antheridia without antheridial branches.

In case of the androgynous species, the antheridial branches begin to appear soon after the oögonial ones (Fig. 21); but the antheridia have usually been formed and come into contact with the oögonium before the basal wall of the latter has appeared. Commonly they are applied by their sides to the oögonial wall, but in a few species (Figs. 54, 94) they present their ends, so that their longer axes are nearly at right angles with the wall, instead of parallel with it, as in most species.

When a certain stage in the differentiation of the contents of the oögonium has been reached, as will be described later, the antheridia give rise, in most cases, to slender tubular outgrowths from the sides applied to the oögonial wall. The tubes penetrate this wall and grow into the cavity within, remaining simple or branching. These structures are, morphologically at least, fertilization tubes. In species with pitted oögonia the antheridia are often, but not always, applied to the thin places, and the fertilization tubes can thus penetrate more easily. But the old view that the pits are perforations of the membrane for the admission of these tubes is untenable from any point of view.

The sexual organs are, then, specialized branches; but their special character does not prevent their showing occasional reversional features, recalling their primitive nature. The oögonial branch may subdivide and bear an oögonium on each division (Fig. 22). It is not uncommon to see a young oögonium which has ceased its normal development and produced one or more smaller oögonia by proliferation from its surface (Fig. 23); and I have seen in *A. Americana* a fully formed oögonium, which, after the formation of its basal wall, had reverted to the vegetative condition, so to speak, and had given rise to an oögonial and an antheridial branch which had reached their full normal development (Fig. 24). The production of an antheridial branch from the very body of an oögonium occurs so commonly as to be normal in *A. racemosa* (Fig. 96), in which the branch arises as often above the basal wall of the oögonium as below it; but the antheridium is probably cut off from its branch before the oögonium is cut off. Further proof that there is no fundamental difference between the two kinds of sexual branches may be found in the fact that antheridial branches may produce at their ends small, though abortive, oögonium-like swellings, even after giving off branchlets with normal antheridia (Fig. 25). I believe I have also seen the formation of a spore-like body in a similar swelling, as observed by Zopf ('90) in *Peronospora calotheca*, but have not been able to feel certain on this point.

Having now traced the origin of the sexual branches and the formation of the sexual organs in general, we pass to the detailed examination of the fate of their protoplasmic contents. The dense mass of protoplasm which fills the oögonium when it has attained its final form, contains, like that of the sporangium, very numerous

nuclei irregularly scattered through it. The protoplasm is at first pretty evenly distributed through the cavity of the oögonium, and encloses irregular vacuoles. But it soon forms a definite parietal layer which is densest next the wall, and the vacuoles fuse into a single large central one. The nuclei are still indefinitely arranged (Fig. 30). They vary considerably in size, and in structure are identical with those of the vegetative filaments from which they are derived. After the growth of the oögonium has ceased and the protoplasm has become parietal in position, the outer walls thicken and the basal wall is formed, as already described.

After an interval the parietal protoplasm begins to undergo changes preliminary to becoming collected into one or more globular masses. We owe our first exact knowledge of these phenomena to DeBary ('81), who studied them in several species. The figures here given of the later stages of the process in a species not studied by him, *A. apiculata*, may serve at least to corroborate and supplement his account and illustrations (Figs. 26, 27). The first change observed consists in the appearance in the protoplasm of numerous light spots, approximately circular in surface view, which may be seen to slowly shift their positions and eventually to disappear. These spots were thought by Pringsheim ('58) to mark the positions of future pits in the wall, which he regarded as perforations formed by resorption. Reinke ('69), Cornu ('72), and DeBary ('81), showed that the spots are much more numerous than the pits and that they occur in all species without regard to the structure of the wall. It is undoubtedly true that they are much more numerous than the pits in pitted oögonia and that they bear no relation to them. DeBary's explanation ('81) of their nature is supported by their appearance in section (Fig. 32). They are doubtless the expression of vacuoles in the parietal protoplasmic layer, formed by accumulations of cell-sap, and finally empty into the central vacuole. Thus the central cavity becomes gradually larger and the wall-layer correspondingly thinner and denser (Fig. 33). The upper vacuole in Fig. 32 has united with the central one in Fig. 33. After the vacuoles have disappeared, the proper degree of density having been reached, as we may suppose, the protoplasm begins to flow towards certain regions and away from others, causing a heaping up at the former and a thinning at the latter places. These accumulations increase at the expense of the surrounding material until there are formed a number of pretty distinct masses connected by a thin parietal sheet of protoplasm, which is still a continuous lining of the wall (Fig. 26, *a*). This layer now breaks and its rupture is followed by a large increase in the volume of the protoplasmic masses, corresponding to the stage of swelling in the sporangium. At the same time, the basal wall, previously convex downward, becomes reversed in position, indicating a loss of turgescence, as in the sporangium; and the fragments of the parietal lining

are absorbed into the masses, which we may call, following the homology of the sporangium, oösphere-origins (Fig. 26, *b*). If the rapidly shifting vacuoles present in the sporangium at this stage are also formed here, the protoplasm is too dense to permit their recognition. The oösphere origins, which, when numerous, may nearly fill the oögonium at their period of greatest swelling, now contract rather rapidly, approaching more and more nearly to the spherical form. During this process there are separated from the origins small masses of protoplasm which may move away a short distance and may remain detached for some minutes (Fig. 26, *c*); but they appear to be always taken up again by the same origins from which they were separated (Fig. 26, *d*). The rounding off is soon completed, and the oögonium contains a number of fully formed oöspheres. All the oögonia of some species, and the smallest of most others, produce only a single oösphere in each. The formation of these follows the same course as that above described for the polysporic oögonium, with certain necessary simplifications. As has been intimated, the oöspheres are normally spherical, but they may assume an ellipsoidal or cylindrical form when compelled to do so by the size and shape of the space within which they are developed.

The separation of protoplasmic fragments from the zoöspores and oöspheres during their final contraction and rounding off, and their subsequent reabsorption by their parent masses, constitute phenomena of peculiar interest. They were first observed by DeBary ('81) in connection with the oöspheres, where they are the more conspicuous; and their formation has been regarded as analogous with that of the polar bodies of the animal egg, while their reabsorption has been explained as compensating for the absence of an act of fertilization. But the fact that the nuclei of the oöspheres are reduced to one or a very few at the time of their formation makes it certain that these fragments are non-nucleate and therefore not analogous to polar bodies; while the fact of their separation from the zoöspores also removes the possibility of their sexual significance. They probably represent in their formation the persistence of some inherited phenomenon of no present functional significance, as Hartog ('92) has suggested.

It will be seen that, omitting the preliminary formation of vacuoles, the changes which characterize the formation of the oöspheres are identical with those observed in the development of the zoöspores. But the time required for the former is much longer, for the zoöspores may escape an hour after the cutting off of the sporangium, while the oöspheres may require eight hours or more for their formation.

As soon as the oöspheres are differentiated, the antheridia, when present, begin to produce the fertilization tubes, which soon reach and come into more or less close contact with the former. The tendency of the tubes to grow towards the oöspheres

and to attach themselves to them is clearly marked, but does not appear to be so strong and invariably active as it has been said to be by most writers.

Each oösphere now secretes about itself a delicate cellulose wall, which gradually increases by successive deposits until it attains a considerable thickness. From the time of the appearance of the wall these bodies are no longer oöspheres, but oöspores. The fertilization tubes soon begin to fade and finally quite disappear, as do also the antheridia and even the antheridial branches, in some species.

By the earlier writers it was assumed from the fact of their presence and from the analogy of related fungi, that the tubes are functional organs of impregnation and that an actual fertilization occurs. Some, especially Pringsheim ('55, '58, '60), argued for the necessity of fertilization. This author at one time ('60) regarded certain peculiar filaments, whose peculiarity was really due to Chytridiaceous parasites, as male filaments of species which have no antheridial branches; but later ('74), he gave up this view and considered plants of the latter sort as parthenogenetic forms of sexual species. Reinke ('69) described uniciliate spermatozoid-like bodies as the fertilizing element in *S. monoica*. These were probably zoöspores of *Chytridiaceæ*. Cornu ('72) assumed and argued for the necessity of fertilization, and maintained the inability of unfertilized oöspheres to form ripe oöspores. Doubt of the existence of functional sexuality in these fungi was first expressed by DeBary ('81) and was based on his failure to observe any passage of material from tube to oösphere, or even any opening in the tube. Pringsheim ('82) opposed these views very strongly with arguments and with an account of observations of the penetration of the oöspheres by amœboid swimmers—"spermamœbæ"—developed in the fertilization tubes and set free from them. Zopf ('82) described amœboid parasites of *Saprolegniaceæ* and attributed Pringsheim's spermamœbæ to this source. Ward's observations ('83), while not extensive, confirmed DeBary's. The further discussion of the subject consisted simply in the maintenance of their former positions by those engaged, and may be followed in subsequent papers of DeBary ('83), Pringsheim ('83, '83a), Müller ('83), and Zopf ('83). The result has been that the conclusions of DeBary have generally been adopted and made the basis of discussions of the group. The writer has attempted to investigate the question independently in connection with the cytology of the sexual organs, to which we may now turn.

The structure and nuclear changes of these organs have been studied chiefly in the genera *Saprolegnia* and *Aphanomyces* by previous writers, and by the present one chiefly in *Achlya Americana* and *A. apiculata*. The method employed in these investigations has been that of serial sections. Flies well covered with hyphæ of the species to be studied, bearing abundant sexual organs in various stages of develop-

ment, were fixed with a saturated aqueous solution of picric acid for twenty-four hours, in the earlier part of the work. Later, this treatment was replaced by exposure for fifteen or twenty minutes to a hot saturated aqueous solution of corrosive sublimate (HgCl_2). This reagent fixes the cell contents without even the slight distortion caused by picric acid, and is strongly to be recommended for such work, as has been done by Hartog ('89a). The whole specimen was, after fixation, washed and soaked in fifty per cent. alcohol, and then stained for twenty-four hours in Grenacher's or Kleinenberg's hæmatoxylin. After being washed again and passed through graded alcohols and chloroform into paraffin, in the usual manner, the fly with attached fungi was imbedded in paraffin and cut into sections about 7μ in thickness by means of the Minot microtome. The sections were then mounted serially in balsam.

The very numerous nuclei carried into the young oögonium with the protoplasm exhibit the structure of the mycelial nuclei, as has been said (Fig. 30). The number of these nuclei bears no relation to the number of oöospheres to be formed, except as both are controlled by the amount of protoplasm in the oögonium. In nine sections, including the whole of a young oögonium, about 60μ in diameter, of *A. apiculata*, I have counted 175 nuclear structures. With liberal allowance for the presence of parts of the same nucleus in two sections, it is not probable that the oögonium contained less than 100 nuclei; yet this species rarely produces more than five oöospheres in an oögonium. The nuclei remain passive during the formation of the central vacuole, and finally lie distributed through the parietal layer (Fig. 30). I have never been able to see any evidence of division in oögonial nuclei, and believe, with Hartog ('92) and Dangeard ('90), that it does not occur. After the formation of the parietal layer, the nuclei appear to migrate towards each other and to fuse in pairs (Fig. 31); and a little later they are seen to be much less numerous and larger, as well as far less deeply stained by hæmatoxylin (Fig. 32, 33). Indeed, a careful search with well-managed illumination is necessary for their detection. This is due to the fact that their chromatin masses largely lose their characteristic power and are masked by the granular protoplasm, while the nuclear membrane becomes barely recognizable. The space between the membrane and the chromosome, occupied by the hyaline part of the nucleus, is proportionally larger than in the vegetative nuclei; and it is probably this fact, combined with the faintness of the other parts, that has led Hartog ('89) to attribute to these fusion-nuclei the vacuolated appearance of the young oögonium. That the two conditions are quite distinct, though occurring simultaneously, as Dangeard ('90) has maintained, may be seen in Fig. 32. The observed reduction in the number of the nuclei is plainly due to nuclear fusions (Fig.

31), probably many times repeated, but whether all the original nuclei are involved in these fusions, or whether some of them degenerate and disappear like those of the periplasm of *Peronospora*, as described by Wager ('89), is uncertain. When the protoplasmic layer reaches its greatest density and regularity of arrangement, the nuclei are in this indistinct condition (Fig. 33). Just when and how they regain the vegetative structure, I am not yet able to say, having unfortunately failed to obtain sections of oögonia at the stage of the formation of the oösphere origins and of the rounding off of the oöspheres. It is certain, however, that, as Hartog has said ('89), and contrary to the statements of Dangeard ('90), the young oöspores contain but a single rather large nucleus (Fig. 35). This is commonly true also of the fully formed oöspheres, but sometimes these contain two nuclei which have not yet fused, though usually lying near together (Fig. 36). Hartog ('92) states that in *Saprolegnia* the reduction of the number of nuclei to that of the future oöspheres is completed as early as the beginning of the formation of the origins, while in *Achlya* it may be delayed until the young oöspore. My observations agree with these so far as *A. Americana* is concerned, but I have not examined any species of *Saprolegnia*. The single nucleus, or the two which are to form it, shows the structure and reactions of the vegetative nuclei.

Although its protoplasm is little denser than that of the vegetative threads, the antheridium is plurinucleate (Fig. 34, *a*). When the fertilization tube is formed, most of the protoplasm and usually all of the nuclei of the antheridium pass into it (Fig. 34, *a*). Hartog states ('92) that the nuclei of the tubes are derived by division from those of the antheridia; but, so far as *A. Americana* is concerned, I have seen no reason for supposing that nuclear divisions occur here more than in the other reproductive organs. The number of nuclei in different antheridia of this species does not vary widely, and the number in a tube corresponds pretty closely, as a rule, to the number in an antheridium (Fig. 34, *a*); and as the growth of the fertilization tube is accomplished apparently by the migration of the protoplasmic contents of the antheridium, and not by any increase in its amount, there is no *a priori* reason for nuclear division, under the circumstances. After passing into the tubes, the nuclei undergo no change. It is occasionally possible to find a fortunate section through the sexual organs and oöspores, like that figured in Fig. 34, *a*, which shows well their relations and the fate of the tubes. And one always finds that, in whatever stage of development the oöspores may be, the tubes are completely closed, as was stated by DeBary ('81), and show their walls sharply defined throughout; and that their protoplasm and nuclei are in essentially the same condition until they begin to degenerate after the complete ripening of the spores. One sometimes observes a nucleus in

the very end of the tube after the wall of the oöspore has become thick and dense (Fig. 34, *a*). Since it is impossible to accept any view of fertilization which does not involve the passage of a nucleus from the tube, these facts must remove all possible doubt of the correctness of the belief expressed by DeBary that these fungi are no longer truly sexual, in spite of their fully developed sexual organs.

After the thickening of its wall, a period of a few days is necessary for the complete ripening of the oöspore. The visible sign of this process lies in the separation of the fatty material, which has been until now scattered in small globules through the protoplasm, into one or a few large and more or less spherical masses. While in certain species it characteristically remains in several portions (Fig. 68), it is commonly fused into a single drop (Fig. 111). This generally continues surrounded by protoplasm and nearly central (Figs. 95, 111), although it may be so much displaced as to leave only a thin film of protoplasm over one side. Oöspores of this type are called centric, to distinguish them from those of excentric structure, in which the oil globule or globules and the protoplasmic mass occupy opposite sides of the spore, and are in contact only by their margins (Figs. 68, 73).

After a period of rest which varies greatly in different species, the oöspores may germinate. Preparation for this process consists in the breaking up of the oil globule and its rediffusion through the protoplasm. The inner membrane of the spore now grows out through a rupture in the outer one into a short thread similar in structure to a vegetative hypha (Fig. 29, *a*). If this thread comes at once into contact with available nourishment, it may develop rhizoids and branch, and so grow directly into a new plant. But if nourishment be not immediately at hand, the hypha, after a brief growth, forms a sporangium at its apex in the manner typical of its genus. There can be no doubt that the numerous nuclei of the germ-hypha arise from the division of the single nucleus of the oöspore, but how early the division begins is not certain. Dangeard ('90) maintains that the oöspores are always multinucleate, and it may be that this division begins, at least in some species, quite early, and that therefore he has overlooked the uninucleate stage. He suggests that a difference may be found between oöspores which germinate at once and those which require a considerable period of rest. But there is no doubt that the oöspores of *A. apiculata*, which, according to DeBary ('84), germinate as soon as they are ripe, are distinctly uninucleate.

In comparing the chlamydospores and the oögonia of the *Saprolegniaceæ*, we may assume what is probably true, that no nuclear changes occur within the former. If

so, then the only real differences between these two organs are found in the concentration of the protoplasmic contents of the latter into one or several separate masses and the fusion of the nuclei of these masses into one, to be restored by subsequent division. These differences are of purely physiological and sexual significance and are inheritances from the truly sexual ancestors of these plants. But on the other hand, it is evident that sporangia, chlamydospores, and oögonia are strictly homologous organs.

It is easy to speculate upon the relationships of the present family to various other groups of *Algæ* and *Phycomycetes*; but this would be of little profit. Until our knowledge of some details of the development of the plants concerned, especially of their cytology, is more complete, it seems well to refrain from further conjecture.

OCCURRENCE AND DISTRIBUTION.

The *Saprolegniaceæ* are found more or less commonly in all fresh waters, but prefer such as are pure and clear. They occur most abundantly and develop most luxuriantly in such waters as contain and favor the growth of the pure-water *Algæ*, *Conjugatæ* and *Chlorophyceæ*. In stagnant waters or those which are polluted by organic matter, they may be found, but their development is usually slow and feeble, and is often quite arrested by the swarms of *Bacteria* and *Infusoria* which find their congenial conditions in such places. The most striking exception to this general statement is afforded by *Leptomitus lacteus*, which grows especially in waters containing considerable organic impurity; and the same is perhaps true of the other *Leptomiteæ*.

These plants are usually saprophytic and grow upon animal and vegetable remains. The latter may include dead, woody or herbaceous parts of vascular plants or even decaying *Algæ*. On the last I have found *L. lacteus* growing vigorously. But it is on animal remains that they flourish best; and of these the most favorable appear to be insect bodies. The reason for this fact probably lies in the circumstance that these bodies, being protected by a chitinous skeleton, are not so exposed to the attacks of putrefactive *Bacteria*, and therefore decompose slowly and cause little pollution of the surrounding water, as compared with a bit of naked flesh of the same bulk. The *Saprolegniaceæ*, too, undoubtedly act as scavengers in appropriating for their own growth the more readily available organic compounds of the dead body. In cultures in a small volume of water, the evidences of decay disappear after a few days, coincidently with, or even before the cessation of active growth in the fungus, consequent upon the exhaustion of available nourishment.

One or more species of the group are facultative parasites which can attack living fishes and Amphibia, and cause serious disease which usually results in death. Under certain conditions which are not yet well determined, the disease may become epizootic and cause great mortality in a lake or stream or in some restricted part of it. Notices of such cases occur throughout the literature from the time of Hannover ('39) and Unger ('43) to the present. The most famous outbreak, and the one best studied, was that on salmon and some related fishes in the rivers Esk, Eden, Nith, and others in England and Scotland. The details concerning this attack and concerning the pathology of the disease may be found in the papers of Smith ('78), Stirling ('78, '79, '79 a), Brook ('79), Buckland ('80), and Huxley ('82). It is sufficient to say here that Huxley was convinced that the disease was caused by a truly parasitic *Saprolegnia*, called by all writers on the disease, *S. ferax*. The only reference to the occurrence of a similar epizootic in America which has come to my notice, is a brief note by Gerard ('78), who reported severe mortality among fishes, from this cause, in the Passaic river in New Jersey.

Murray ('85) and Schnetzler ('87) have found that the zoöspores of "*S. ferax*" cultivated on flies can attack living fishes and frog-tadpoles and produce a growth of the fungus which kills the victim. Some facts concerning the effects of *A. racemosa* in a fish-hatchery will be discussed in connection with the description of that species.

Owing to the absence of suitable substrata for their development in mass, and the brief time required for the completion of their life-cycle, these plants are not often found growing spontaneously; and this fact has led to the belief that they are somewhat rare or difficult to obtain. But the writer's experience in the United States fully agrees with that of DeBary in Europe that this is by no means the case. The last-named author has given ('88) very practical hints for obtaining and cultivating them which it will not be superfluous to repeat here, with some additions drawn from personal experience. For reasons above stated, the most prolific source of supply is water containing green Algæ, and the best substratum is afforded by insects such as common house-flies or meal-worms. For material, a handful of Algæ may be taken from the stream, pond, or pool in which they are growing and placed in a collecting bottle or other vessel which will protect them from drying. In the laboratory, these are placed in a vessel of water from the public or private water supply, and the culture insects are thrown upon its surface. The collection of a mass of Algæ without water, except that retained by the mass, reduces the bulk of specimens, which is of importance when they are taken at a distance from the laboratory, and largely excludes aquatic organisms which might make trouble in the cultures; while experience shows

that the zoöspores and oöspores of the *Saprolegniaceæ* are carried with the Algæ to a large extent. If it is desirable to avoid any possible infection from other sources than the mass of Algæ concerned, the water may be filtered, heated to boiling, and then cooled, before the specimen is placed in it. DeBary found that, in practice, the water supply of Strassburg never produced any of these fungi in cultures made with water from its pipes alone; and I have had the same experience in repeated trials with that of Amherst. But water from the Cambridge pipes, and doubtless that from others, will yield them at certain seasons, at least. The insects used may be freshly killed, and their chitinous covering should be broken as little as possible; but I have found that, for winter cultures when fresh insects are not readily available, an excellent substitute may be found in dead house-flies, collected in the fall and kept dry and exposed to the air, but protected from dust. Since the dry surfaces of insects are not readily wetted by water, it has proved useful to moisten them, whether fresh or dried, with alcohol, and then to soak them in water for a few minutes to remove the alcohol. They will then, when thrown into the culture vessel, sink until their bodies are mostly below the surface and so present a much larger area to the swimming zoöspores of *Saprolegniaceæ* than if dry and floating largely above the surface.

Since the zoöspores depend for their activity on a sufficient supply of oxygen we may expect them to be most abundant near the surface of the water, and since they are chemotactic, being strongly attracted by nutrient substances, they must readily reach the floating insects and germinate upon their bodies. An average time for the appearance of the young hyphæ is perhaps two days from the beginning of the culture, but one day is ample time, as a rule, for the zoöspores to have effected an attachment to the substratum. The insects should now be transferred to a vessel of fresh, clean water, and here the development of the fungus may be followed. The water should be carefully changed daily or less often, as may be required, until the maximum of vegetative activity is past. For superficial examination, the whole insect with attached fungi may be floated upon a slide. For more thorough study, parts seen by this preliminary method to be in the desired condition may be cut off and mounted under a cover, or used for a hanging drop culture. Rothert ('88) has pointed out that well-grown filaments with reproductive organs continue to develop normally after being cut off, until their protoplasm is exhausted.

It is not easy, although it is usually possible, to obtain from a mixed culture of several species, pure cultures of each. This may be accomplished by using sterilized water, fresh, clean insects, well-soaked in alcohol and distilled water, and a very small quantity of the fungus, preferably zoöspores from a single sporangium. A few attempts will give the desired result, if the first does not. The use of small portions

of successive cultures is very useful here, as in the culture of Bacteria, in eliminating all but a given form. Many species grow well on a flooded slide in the saturated atmosphere of a moist chamber. Cultures may be pretty safely sent by mail in suitable mailing tubes for liquids, but should be sent at the proper stage of development. After some experience in this matter, it appears to the writer that the best time for mailing a specimen which will be more than a day *en route* is when the sexual organs are just fully formed. They should be placed in a tube filled with clean, preferably sterilized, water and mailed at once. If sent later, the plants are likely to fall in pieces on the way ; while, if sent earlier, the close confinement for some time and the consequent vitiation of the water seem to reduce their vigor so that they subsequently fail to produce sexual organs.

The application of the above described culture methods to American materials has shown, as has been said, that these plants are not less abundant with us than in Europe. Among the many samples of material from the most varied sources, which he investigated, only one failed to furnish to DeBary some member of this family. In a large number of cultures from fresh waters of all kinds, rivers, ponds, brooks, spring-holes, drains, and rain-pools of brief duration, in short, from wherever Algæ appear, I have failed only two or three times to obtain *Saprolegniaceæ*. A single culture may often yield several species. DeBary gives seven as the largest number obtained by him from any one source. I have obtained nine species from two handfuls of moss and Algæ from a small shallow pool just at the border between a swamp and damp pine woods. On dead branches in this pool grew *Mougeotia* sp. and *Ulothricaceæ*, and over the mosses bordering it crept the filaments of a species of *Tolypothrix*. Cultures produced at once *S. diclina* and *torulosa*, *A. Americana*, *apiculata*, *racemosa*, var. *stelligera*, and *papillosa*, *Dictyuchus* sp., and *L. lacteus*. After the material had stood in an open jar near a north window for a few months, the green Algæ had disappeared, but the mosses and *Tolypothrix* had grown freely. Flies dropped into the jar soon bore *Aph. lævis* in abundance.

It is not yet possible to generalize at all concerning the distribution of the species of this family ; but it seems probable that a great majority of them are likely to prove cosmopolitan. One difference has been very conspicuous, however, in the cultures I have studied ; namely, that in those from the Northern States there has been a distinct predominance of species of *Achlya*, while in those from the Southern States specimens of *Saprolegnia*, if not different species, have been far more abundant.

The following synopsis of American species can, of course, be only a fragmentary representation of our flora, since it covers but few localities and these only in a

desultory way. But the fact that of the thirty-four established European species, sixteen are here included, while five species previously unknown are described, shows what we may expect as the result of thorough exploration of many localities. It is hoped that the present contribution may serve to stimulate such exploration.

HISTORICAL.

The first references to any of the *Saprolegniaceæ* appear to have been those of Ledermüller in 1760, of Wrisberg in 1765, and of Spallanzani in 1777. By these and later writers for a long time they were regarded as Algæ and were described by most under the generic name *Conferva*, which included, in its Linnæan application, the filamentous aquatic plants, generally. The earliest binomials appear to be those of the Flora Danica (1780), *Byssus aquatica*, and of Schrank (1789), *Conferva piscium*. Previous writers had seen these fungi on flies in water, but in Schrank's name is the first record of their occurrence on fishes. The earliest figures are those of the Flora Danica (1780), of Dillwyn ('09), and of Lyngbye ('19). As the early observers saw and figured only the sporangia, it is impossible to refer their plants to the proper species. It can only be said that the names *Byssus aquatica* Fl. Dan. and *Vaucheria aquatica* Lyngb. refer to species of *Achlya*. Dillwyn figured the *Conferva lactea* of Roth (1789), which is recognizable as our *Leptomitum lacteus* Ag. Gruithuisen described ('21) a fungus on the remains of a dead snail, and for the first time figured the escaping zoöspores of *Saprolegnia*, though without cilia. This form he called *Conferva ferax*, a name which was subsequently used promiscuously by many authors for any of the larger species of this family. It was first applied to a distinctly characterized form by Thuret ('50), though without an understanding of the real specific differences among these plants. Carus next ('23) described a fungus on salamander larvæ, with spores collecting in a globe at the mouth of the sporangium, which he called *Hydronema*. He observed several characteristic features in the development of the form, and recognized its points of difference from Gruithuisen's fungus. In an appendix to Carus' paper, Nees von Esenbeck ('23) established the genera *Saprolegnia* and *Achlya* on the distinctive differences in the escape of the zoöspores which we recognize as their most salient characters, to-day. He called Gruithuisen's fungus *S. molluscorum*, and Carus' form *A. prolifera*; but he apparently did not know the sexual organs, and it is impossible to identify the species intended by him. A year later, Agardh ('24) included in his genus *Leptomitum* all described *Saprolegniaceæ* under the names *L. clavatus*, *prolifer*, and *ferax*, grouping the forms of earlier writers rather according to substrata than by structure, and mix-

ing his synonymy confusedly. Berkeley ('33) followed Agardh's generic arrangement, and called the form he figured *Leptomitius piscidicola*.

After brief and unimportant mention of these plants in earlier papers, Meyen described ('39) some features of the development and escape of the spores and of their germination. He also observed dictyosporangia. Now followed a series of accounts of observations concerning the attacks of *Saprolegniaceæ* on aquatic Vertebrates by Hannover ('39 and '42), Stilling ('41), Bennett ('41), and Goodsir ('42). These papers contained little of real importance except Hannover's second one, which has been before mentioned as containing the first good account of the development and later history of the zoöspores. Unger's account ('43) was in some respects less complete than that of Hannover. All the writers yet mentioned dealt only with the sporangia, in most cases of the *Saprolegnia* type; but nearly all called their plants *Achlya prolifera*. In Schleiden's "Grundzüge" ('45), we find the first account of a second and larger sort of spores, which we now know as the oöspores. These were again mentioned by Naegeli ('47) and by Braun ('51), the latter of whom also described the antheridial branches. Naegeli ('47) speaks of a third sort of reproductive organs, which were probably, like those described by Cienkowski ('55) the sporangia of parasitic *Chytridiaceæ* of the genus *Olpidiopsis*. The general features of the development of both sporangia and oögonia were described at this time by Thuret ('50), who then first demonstrated the biciliate character of the zoöspores of *Saprolegnia*, and figured unmistakably the oögonia of the form he studied, which he called *S. ferax*. Now followed those accounts by Pringsheim ('51) and DeBary ('52), which mark the beginning of our exact knowledge of the *Saprolegniaceæ*, and which have led to the long series of contributions, the most important of which are quoted in the morphological and systematic parts of the present paper. The number of these which we owe neither to the researches nor to the direct influence of these two pioneers and masters in the study of the Thallophytes is surprisingly small.

To return to the systematic history of the group: Kützing, in his "Phycologia" ('43), places *L. lacteus*, with various other forms not *Saprolegniaceæ* and largely unidentifiable, under the genus *Leptomitius*, and includes the other forms then known under three species of *Saprolegnia*, *S. minor*, *ferax*, and *xylophila*. In his "Species Algarum" ('49) the same author includes *L. lacteus* as before, and enumerates six additional species of *Saprolegnia*, most of which are now unrecognizable. Braun ('50) established the species *S. capitulifera* for a plant with sporangia of the *Achlya* type. Robin ('53) mentions only *S. minor* and *S. ferax*; and Pringsheim, in his earliest paper ('51), though describing a *Saprolegnia*, calls it *A. prolifera*. It was DeBary ('52) who first again brought forward and applied Nees' old generic distinc-

tions, and showed the necessity for characters drawn from the sexual organs in specific determinations. It is to him and to subsequent writers who recognized the correctness of his position, that we owe our present notions of generic and specific distinctions. No writer before him appreciated the true specific differences, and none save Nees, whose insight remained unrecognized for three decades, saw the true value of characters now recognized as generic. With the single exception of Thuret's *S. ferax*, no species had previously been described or figured so as to be now recognizable. It is an interesting coincidence that his first botanical publication and the posthumous fragment prepared from his last manuscripts by his successor should both have dealt with *Saprolegniaceæ*.

The history of the great progress in the knowledge of this family during the past forty years may be traced, as has been said, in the works referred to on other pages; but certain matters which are now wholly of historical interest may be briefly referred to here. The discussions concerning the specific value of certain morphological differences and concerning the sexuality of these fungi are considered sufficiently elsewhere. But the members of this family have figured prominently in the pleomorphy craze which followed Tulasne's proof of the pleomorphism of many *Ascomycetes*. The extreme advocates of this doctrine, Bail ('60), Hoffman ('67), and Karsten ('69), held that the same plant assumes the form of *Saprolegnia* in water, or of *Empusa* in air, when growing on flies. On other substances the same species was supposed to appear as *Mucor*, or even as *Penicillium*; and in saccharine solutions to take the *Saccharomyces* form. Earlier than these views became popular, similar suggestions had been made. Nees ('31) suggested a connection between *Empusa* and *Achlya*; and Meyen and Cienkowski ('55) affirmed a connection between *Isaria* or *Empusa*, on one hand, with "*Achlya prolifera*," on the other. It is to Brefeld's researches ('71) and the application of rigid culture methods like his that we owe the final proof of the incorrectness of this belief.

The history of American studies of *Saprolegniaceæ* is briefly told. So far as I know, Leidy ('50) first mentioned "*Achlya prolifera*," which he reported having seen in all stages of development on Ascarids in water. Gerard's ('78) brief account of "*S. ferax*" in connection with an epizootic among fish in New Jersey, Hine's ('78) observations on a species of *Saprolegnia* and on *Achlya racemosa*, and Galloway's ('91) cytological notes on *S. monoica* complete the short list.

SYSTEMATIC PART.

The following diagnoses of American species of *Saprolegniaceæ* are drawn wholly from American specimens, except in a very few cases where the incompleteness of

the material has made it necessary to refer to European descriptions for certain details. In all such cases the borrowed matter has been indicated by quotation marks. For species not yet known to be American a brief informal statement of the chief diagnostic characters is given to aid the student who may meet with them, since many of them are likely to be found with us.

Artificial dichotomous keys to all the intelligibly described species are prefixed to the detailed accounts, in all but the smallest genera, as a practical encouragement to their study; but they should never be relied on alone for the determination of species.

SAPROLEGNIACEÆ Pringsh. ('57).

Aquatic fungi, living as saprophytes or facultative parasites, with usually branched mycelium; the hyphæ in a few species constricted at intervals, but remaining unseptate except in the formation of reproductive organs. The latter of two kinds, non-sexual and sexual, both formed from the hyphæ and separated from their vegetative portions by transverse walls. Non-sexual propagation by means of biciliate, often diplanetic, zoöspores, produced in cylindrical or swollen sporangia; or very rarely by homologous non-motile bodies; occasionally also by chlamydospores. Morphologically sexual reproduction by oöspores developed in typically globular oögonia, one or more from the entire protoplasm of each oögonium; antheridia on branches of androgynous or diclinous origin, very rarely on the oögonial branch, uniting with all, or with only a part of the oögonia, or in several species wholly absent; when present, usually producing fertilization tubes which remain closed, at least in some species.

Key to Genera.

- | | | |
|-----|---|--------------------|
| A. | Vegetative filaments with their walls unconstricted..... | ..(Saprolegniæ) B. |
| | Vegetative filaments deeply constricted at intervals..... | (Leptomitæ) I. |
| B. | Zoöspores normally leaving the sporangium by a common mouth..... | C. |
| | Zoöspores not leaving the sporangium by a common mouth..... | G. |
| C. | Zoöspores swarming separately on escaping from the sporangium..... | D. |
| | Zoöspores collecting in a hollow sphere at the mouth, on escaping..... | F. |
| D. | Zoöspores diplanetic; new sporangia growing through the empty ones..... | E. |
| | Zoöspores monoplanetic; sporangia renewed by cymose branching..... | PYTHIOPSIS. |
| E. | Oöspore single, wholly filling the oögonium..... | Leptolegnia. |
| | Oöspores one or more, not wholly filling the oögonium..... | SAPROLEGNIA. |
| F. | Sporangia usually broader than the vegetative hyphæ; zoöspores irregularly arranged..... | ACHLYA. |
| | Sporangia equaling the vegetative hyphæ in breadth; zoöspores in a single file..... | APHANOMYCES. |
| G. | Zoöspores encysting within the sporangium, afterwards swarming..... | H. |
| | Zoöspores encysting and germinating within the sporangium, never swarming..... | Aplanes |
| II. | Zoöspores set free by the breaking up of the sporangial wall..... | Thraustotheca. |
| | Zoöspores escaping each by a separate perforation of the sporangial wall, leaving a "net."..... | DICTYUCHUS. |
| I. | Zoöspores swarming separately on escaping..... | LEPTOMITUS. |
| | Zoöspores collecting at the mouth of the sporangium, on escaping..... | APODACHLYA. |

*Subfamily Saprolegnieæ.***Saprolegnia** Nees ab Esenb. ('23).Syn. : ? *Conferva piscium* Schrank (1789).*Conferva ferox* Gruith. ('21).*S. molluscorum* Nees ab Esenb. ('23).*Leptomitus clavatus* Ag. ('24)." *ferax* Ag. ('24)." *piscidicola* Berk. ('33).*Achlya prolifera* Auct.Exsic. : Myc. Univ., 1213 (*S. ferox*).Algues de la France, 1195 (*do.*).

Hyphæ rather stout or slender, often not much branched. Zoösporangia formed from their tips, generally cylindrical or slightly clavate, rarely short and in series; the later ones arising within the empty membranes of preceding ones by upward growth of their basal walls, or rarely beside them by cymose branching. Zoöspores diplanetic, at first pyriform, with two apical cilia, escaping by a usually terminal mouth at the apex of a distinct papilla, and swarming separately; after encystment and rest becoming reniform swarmers with two lateral cilia; finally encysting again and germinating. Oögonia terminal or intercalary, never wholly filled by the one or more oöspores. Antheridia wholly absent in some species, and always present in some.

Key to recognized Species.

- a.* Oögonial wall always smooth and unpitted; oöspores excentric.....*S. anisospora.*
Oögonial wall pitted, at least in some specimens; oöspores centric.....*b.*
Oögonial wall spiny; oöspores centric.....*i.*
- b.* Oögonia in moniliform series, early falling apart, not all pitted.....*S. monilifera.*
Oögonia not separating from the plants before maturity, all more or less pitted.....*c.*
- c.* Antheridial branches attached to every oögonium.....*d.*
Antheridial branches attached to some or to none of the oögonia.....*f.*
- d.* Plants diclinous; pits small.....*S. DICLINA.*
Plants androgynous; pits large.....*e.*
- e.* Oögonial branch short and straight.....*S. MONOICA.*
Oögonial branch usually helically coiled.....*S. spiralis.*
- f.* Antheridial branches often developed.....*S. MIXTA.*
Antheridial branches very rarely or never developed.....*g.*
- g.* Antheridium formed just below the oögonium, on the same branch.....*S. hypogyna.*
Antheridia not developed, or very rarely so.....*h.*
- h.* Oögonia irregular, often in torulose series, with few and small pits.....*S. TORULOSA.*
Oögonia globular, or not rarely cylindrical, not in series, with large pits.....*S. FERAX.*
- i.* Oöspores one or two in an oögonium; hyphæ slender.....*S. ASTEROPHORA.*
Oöspores several in an oögonium; hyphæ very stout.....*S. TRELEASEANA.*

SAPROLEGNIA MONOICA Pringsh. ('57).

Syn. : *S. ferox* Auct. p. p.*S. dioica* Pringsh. ('60).*Diplanes saprolegnioides* Leitgeb. ('68).*Achlya intermedia* Bail ('60a), sec. Lindstedt ('72).

Ill. : Pringsheim, '57, Pl. XIX, XX.

Reinke, '69, Pl. XII.

DeBary, '81, Pl. V, Figs. 11-19; VI, 1, 2.

Ward, '83, Pl. XXII, Figs. 17-22.

Rothert, '88, Pl. X, Figs. 14.

Pl. XVI, Figs. 37-39.

Hyphæ rather stout, often long. Zoösporangia cylindric-clavate. Oögonia terminal or rarely intercalary, usually on short lateral branches, globular, their walls abundantly and prominently marked with large pits. Antheridia long-cylindrical, uniting with every oögonium, on rather stout branches of androgynous origin, which usually arise from the main hypha near the oögonial branch. Oöspores commonly not above ten, rarely numerous, centric, their average diameter about 26μ .

Massachusetts—Cambridge, *Trelease*; Amherst: Alabama—Auburn, *Atkinson*. Europe.

This species, obtained by Prof. Trelease at Cambridge in 1881, was first procured by the writer from a pool containing dead *Carex* leaves, which bore abundant masses of *Chaetophora*; and subsequently from a mass of dead leaves and slime at the bottom of a ditch draining cultivated fields. Among cultures from the Southern States, it has appeared only once. It does not, therefore, seem to be very abundant with us; but it is well distinguished by the large and numerous oögonial pits and the abundant and well-developed antheridia, which are larger and more conspicuous than those of any other species of the genus, except possibly *S. asterophora*.

The observation of the diplanetism of the zoöspores of this species led Leitgeb to establish a new genus, *Diplanes*, for it, although the phenomenon had previously been observed in species of this genus. Lindstedt gives *Achlya intermedia* Bail as a synonym of *Diplanes saprolegnioides* Leitg., and is followed by Saccardo ('88). Having been unable to examine Bail's description and figure, I must be content with following the authors mentioned.

Var. *montana* DeBary ('88.)

Differs from the type in its slightly or not at all pitted oögonia, on longer branches. It has not been recognized in America.

Saprolegnia spiralis Cornu ('72.)

This form, which appears to have been recognized only by its author, is said to differ from *S. monoica* chiefly in its longer oögonial branches, which are coiled in a

helix of one or two turns. It is of doubtful autonomy, but, in the absence of fuller knowledge, may be allowed to stand for the present; although it would hardly appear to be entitled to more than varietal rank, if well marked.

SAPROLEGNIA MIXTA DeBary ('83).

Syn. : *S. ferax* Auct. p. p.

Ill. : Pl. XVI, Figs. 40-42.

S. ferax Schroeter ('86).

S. dioica Schroeter ('69).

Hyphæ rather slender, not long. Zoösporangia cylindric-clavate. Oögonia terminal or rarely intercalary, on main filaments or lateral branches, globular, with numerous pits of varying size, but often pretty large. Antheridia cylindrical, rather shorter and smaller than in *S. monoica*, of androgynous or diclinous origin, absent from a part of the oögonia, sometimes from a large part. Oöspores up to fifteen or occasionally more than twice that number, centric, their average diameter about 26 μ .

Pennsylvania—Philadelphia, *Keller* : Mississippi—Starkville, *White* : Louisiana—Bayou Tortue, *Langlois*. Europe.

I have not yet with certainty recognized this species in Amherst cultures, but have received it from three sources; which indicates that it is widely distributed and not uncommon. The materials for two of the cultures containing it were taken from small pools, while the third and most abundant specimen came from *Algæ* and *Lemnæ* growing in Bayou Tortue, near St. Martinville, La.

The species is rather vague and unsatisfactorily defined, as DeBary has remarked ('88). It is intermediate in several respects between *S. monoica* and *S. ferax*, and might seem to afford ground for regarding all these as forms of a single species, as Pringsheim does. Having found *S. monoica* and *S. ferax* to be well marked and constant before meeting with this species, I was for some time skeptical concerning it, thinking it might have originated in a mixture of those two. But the receipt of material from distinct sources which could be referred to neither of those, and which shows constantly the characters above stated, in successive generations, has convinced me that the species is well founded and appropriately named. The smaller and less abundant antheridia, not always of androgynous origin, and the usually less numerous and less conspicuous pits of the oögonial wall chiefly distin-

guish it from *S. monoica*. Its hyphæ are also rather slenderer and more flaccid than those of the latter.

The description of *S. ferax* given by Schroeter ('86) is clearly not applicable to that species, but very well characterizes the present one. It must be considered, therefore, that this author's *S. ferax* belongs here as a synonym; and, if so, then also his *S. dioica*, which he quotes ('86) as a synonym of his *S. ferax*. Fortunately, the name *S. dioica* had been used for another plant by Pringsheim ('60) and therefore cannot be retained for this one, although Schroeter's use of it antedates DeBary's.

SAPROLEGNIA FERAX (Gruith.) Thuret ('50).

Syn. : *S. ferax* Auct. p.p.

Achlya prolifera Pringsh. ('51).

S. Thureti DeBary ('81).

Ill. : Thuret, '50, Pl. XVI.

Pringsheim, '51, Pl. XLVI-L.

Pringsheim, '74, Pl. XVIII, Figs. 5 and 11.

DeBary, '81, Pl. V, Figs. 1-10.

Rothert, '88, Pl. X, Figs. 1-13.

Pl. XVI, Figs. 43-45.

Hyphæ of medium size. Zoösporangia clavate-cylindrical. Oögonia terminal or sometimes intercalary on main hyphæ or lateral branches, globular or not rarely cylindrical, their walls very thickly and conspicuously marked by large pits. Antheridial branches and antheridia never developed or extremely rare. Oöspores up to twenty in an oögonium, or sometimes more ("40 to over 50," DeBary), centric, their average diameter about 26 μ .

Massachusetts—Amherst: Wisconsin—Madison, *Trelease*: Missouri—St. Louis, *Trelease*: Kentucky—Lexington, comm. *Keller*. Europe.

In Wisconsin this species was obtained by Prof. Trelease from Algæ collected in a ditch, and at St. Louis it grew spontaneously on flies in water. The Kentucky specimen sent by Dr. Keller was obtained from Algæ, chiefly *Hydrodictyon*, collected in a pool in a cemetery at Lexington. I have never obtained it in Amherst from open-air materials, but have found it on flies thrown in water taken from the room for tropical aquatics in the plant house of the Massachusetts Agricultural College. This specimen was a reduced form in all respects, although undoubtedly of this species.

This plant seems, then, to be more common in the Western than in the Eastern States. The absence of antheridia, the rather common occurrence of cylindrical oögonia, and the very conspicuous pitting of all the oögonia mark the species unmistakably. It was first sharply distinguished and characterized by DeBary ('81), who

called it *S. Thureti*, recognizing it as the form whose oögonia were first figured by Thuret. But although, as has been remarked, the latter author had no understanding of the true specific limits among these fungi, there is still no reason for refusing to restrict to his form Gruithuisen's name, by which he called it, and which had previously been used in a much wider application.

It has already been pointed out that the *S. ferax* (Gruith.) of Schroeter ('86) is probably *S. mixta* DeBary. The description given in Saccardo's Sylloge ('88) under the name of *S. ferax* is quite unrecognizable. It is noteworthy that this work perpetuates the old myth that *Empusa* is an imperfect state of *S. ferax*.

It is difficult to circumscribe what DeBary has called the *ferax* group of *Saprolegnia*, since so many species show relations with each other at various points, while remaining, within their limits, very constant. The three species already described constitute, however, the most closely united group, and it is perhaps better to limit the term to them, if it is to be used at all, than to apply it to an assemblage of species necessarily much larger if at all increased. In these species, taken in the order in which they are here placed, there is observed a progressive reduction in the antheridia, and an increase in the normal size of the oögonia and in the number of oöspores; while the average size of the latter varies little, although extreme specimens may vary as much as 5 μ on either side of the average.

Saprolegnia hypogyna Pringsh. ('74).

Syn.: *S. ferax*, var. *hypogyna* Pringsh. ('74).

Ill.: Pringsheim, '74, Pl. XVIII, Figs. 9, 10.

This species, which has been studied by Pringsheim and DeBary ('88) and is doubtless well founded, differs from all other known *Saprolegniaceæ* in producing antheridia without special antheridial branches. A second portion of the oögonial branch is cut off just below the oögonium and constitutes the antheridium. Its upper wall, which is also the basal wall of the oögonium, grows up, as a fertilization tube, into the cavity of the latter. The oögonia show, in their form, in the pitting of their walls, and in the structure and number of their oöspores, near relations with the *ferax* group, but the species is at once recognizable by the peculiarities above mentioned. It is not yet known to occur in America.

SAPROLEGNIA TORULOSA DeBary ('81).

Ill.: DeBary, '81, Pl. VI, Figs. 3-17.

Pl. XVI, Figs. 46-49.

Hyphæ rather slender. Zoösporangia from cylindric becoming clavate, fusiform, or nearly globular, often in torulose series. Oögonia globular, ovate, pyriform, or

cylindrical, terminal or intercalary, commonly in torulose series, their walls more or less abundantly marked by small pits, and yellowish brown when old. The members of a series may form, some sporangia and others oögonia. Antheridia very rarely present. Oöspores as many as twelve, or rarely more, in an oögonium, centric, their average diameter about 25μ .

Massachusetts—Amherst: New Hampshire—Mt. Washington, *Thaxter*: Louisiana—St. Martinville, *Langlois*. Europe.

A characteristic species which is not very uncommon with us, apparently. In my Amherst cultures it has appeared twice, once from the very prolific mossy pool, mentioned elsewhere, and again from algæ (*Spirogyra*) from a small boggy area by a brook. Prof. Thaxter has sent me specimens developed spontaneously on Lepidopterous larvæ in the "Alpine Garden," on Mount Washington; and Mr. Langlois has obtained it from a ditch in Louisiana. It shows some points of affinity with the *ferax* group, as here limited, yet is very distinct. The antheridia have not disappeared quite so completely as in *S. ferax*; and the oögonia contain less numerous oöspores, while their walls are much less pitted and are more deeply colored when mature than in any of the previous species. American specimens do not quite meet DeBary's character, "mit wenigen oder ganz ohne Tüpfel," as they always have, so far as my observation of a large number of individuals goes, some pits, and often a considerable number; but these are always small.

The best diagnostic character of the species is found in the successive formation of walls in the same filament, cutting off as many segments, which may all become sporangia, or all oögonia, or partly each. In the latter case, the terminal members usually become oögonia. The oögonia remain attached to the plant until the hyphæ become disorganized, and therein differ from those of the next species. No better evidence could be desired of the lack of fundamental difference between sporangia and oögonia than the indiscriminate formation of both from exactly similar members, at the same time, here observed.

Saprolegnia monilifera DeBary ('88).

Ill. : DeBary, '88, Pl. IX, Fig. 6.

DeBary separates this species as a distinct type from the other members of the genus, although, judging from his description, it would seem to represent a further development on the lines of *S. torulosa*. Its oögonia are formed in somewhat more definite moniliform chains, all of whose members appear to have the same fate.

Their walls are occasionally pitted, and no antheridia are developed. A striking feature is the separation of the oögonia from the plant and from each other, often at a very early stage, so that they lie free in the water and complete their development independently.

The species presents a transitional feature leading towards *Achlya*, or a reversal towards the commonest condition in the family, in that many of the later sporangia are produced by cymose branching, instead of by the usual method for *Saprolegnia*. It has not been seen in America.

SAPROLEGNIA DICLINA nom. nov.

Syn.: *S. dioica* DeBary ('88).

nec *S. dioica* Pflingsh. ('60), nec Schroet. ('69).

Ill.: DeBary, '88, Pl. X, Figs. 12, 13.

Pl. XVII, Figs. 50-53.

Hyphæ slender, not long. Zoösporangia nearly cylindrical. Oögonia terminal on main hyphæ, or less commonly on lateral branches, typically globular, their walls marked with small pits, which are often few and inconspicuous. Antheridial branches long, flexuous, and very slender, of diclinous origin. Antheridia on every oögonium, ovate or short clavate, often very abundant and covering much of its surface, sometimes rather few. Oöspores most commonly ten or twelve, sometimes twenty or more, and often only four to six, centric, their average diameter about 25 μ .

Massachusetts—Amherst: Pennsylvania—Philadelphia, *Keller*: Alabama—Auburn, *Atkinson*: Louisiana—St. Martinville, *Langlois*. Europe.

This is unquestionably our commonest *Saprolegnia*. I have obtained it six or seven times in cultures from small pools, spring-holes, and similar places, and have received it from most of my correspondents, as above shown. It is readily identified by the small and fewer pits of the oögonial wall, as compared with those of the *ferax* group; and especially by the antheridia, which are always present, as in *S. monoica*, but smaller, of different shape, and on slenderer branches than in the latter species; while the branches are always of diclinous origin. When the plants become old, these delicate antheridial branches often disappear, leaving the antheridia adhering to the oögonia without indication of their origin. This may, indeed, happen in other species, but not so commonly or so early as in the present one.

A reduced form of this species, hardly worthy of varietal rank, occurs frequently. It is distinguished chiefly by its smaller size, and by a reduction of the number of both oöspores and antheridia to a very few (Fig. 53).

The species, as limited in America, is exactly *S. dioica* DeBary, except that I

have never seen the intercalary barrel-shaped oögonia, said by that author to occur sometimes. It should bear his name, but for the fact that that name had previously been applied by Pringsheim ('60) to *S. monoica* attacked by Chytridiaceous parasites; and this previous use of the name, although it can stand only as a synonym, should debar its further use, in the interest of clearness and accuracy. The use of the same name by Schroeter ('69) for apparently another species has been already alluded to. It may be, as DeBary intimates ('88), that this species has been included by some authors under the name *S. dioica*; but there is not the least evidence that the original author of that name even knew it. In order to change its name as little as possible, and yet sufficiently, I propose for the species that of *S. diclina*, which refers to the same peculiarity as did the former one.

An error which has been overlooked in reading the proof of Saccardo's Sylloge ('88, p. 269) makes what is intended for *S. dioica* read *S. divisa*. The description which follows refers to Pringsheim's pseudo-species.

Saprolegnia anisospora DeBary ('88).

Ill.: DeBary, '88, Pl. IX, Fig. 4.

This European species takes its name from the fact that its sporangia are of two kinds, producing respectively large and small zoöspores. These are said to agree perfectly in structure and development, but the larger are of about twice the diameter of the smaller, which are like those of other species of *Saprolegnia*. The oögonial walls are unpitted and the antheridia agree with those of *S. diclina* in their form and in their diclinous origin. This is the only known *Saprolegnia* which has excentric oöspores. DeBary well remarks that the species deserves further study.

SAPROLEGNIA ASTEROPHORA De Bary ('60).

Ill. : DeBary, '60, Pl. XX, Figs. 25-27.

DeBary, '81, Pl. VI, Fig. 18-29.

Pl. XVII, Figs. 54, 55.

Hyphæ slender, "with cylindric-clavate zoösporangia." Oögonia terminal, globular, with several or many rather long, blunt outgrowths of the wall, giving it a starlike appearance; the wall unpitted. Antheridia "usually present," on branches arising just below the oögonia from the oögonial branches, short-clavate, applied by their ends. Oöspores commonly single, sometimes two or rarely three, centric, thick-walled, their diameter about 30μ .

Massachusetts—Cambridge and Wood's Holl, *Trelease*. Europe.

I have never had the opportunity of studying this species alive, and hence arises the necessity for referring to DeBary's description ('88) for some details. It occurs in preparations made by Prof. Trelease from cultures made in Eastern Massachusetts, and must therefore be included in our flora. It has hitherto been the only known member of the genus with spiny oögonia, and is readily distinguished from the second such species, next to be described, by its globular and few-spored oögonia, borne on slender threads.

SAPROLEGNIA TRELEASEANA sp. nov.

Ill. : Pl. XVII, Figs. 56-59.

Hyphæ very thick. Zoösporangia cylindric, rare. Oögonia terminal or intercalary, on main hyphæ, elliptical or globular, when terminal usually ending in a strongly developed apiculus; their walls not pitted, but with rather scattered blunt outgrowths of varying length, oftenest short. Antheridial branches short and slender, arising just outside the oögonial wall, one or several to each oögonium, or sometimes wholly absent. Antheridia short-cylindric or slightly clavate. Oöspores numerous, averaging ten or twelve in an oögonium, centric, their diameter from 25 to 35 μ .

Massachusetts—Wood's Holl, *Trelease*.

It is a great pleasure to dedicate this very striking species to its discoverer, Prof. William Trelease, of St. Louis, whose early studies of our *Saprolegniaceæ* were unfortunately cut short by other engagements. This is done as a slight acknowledgment of the valuable additions to the present paper which are due to his generosity, and in recognition of the high character of his work as a botanist.

The species was obtained by him in 1881 in cultures with material from Wood's Holl, Mass., and he has communicated all his notes and material to the writer. It has very coarse and freely branched hyphæ which often considerably exceed 100 μ in diameter at the base. The sporangia are so rare that Prof. Trelease observed only one (Fig. 56), and I have been unable to find any in his material. The size and manner of branching of the hyphæ, as well as the appearance of the oögonia, strongly suggest the genus *Achlya*, but the single sporangium seen showed that the spores escape as in *Saprolegnia*. In the structure of its sexual organs this plant resembles quite strikingly that to be described later as *Achlya papillata*, but it is

much more robust than that and sufficiently distinct otherwise, aside from the differences in the sporangia.

SPECIES INQUIRENDÆ.

Saprolegnia androgyna Archer ('67.) See Notes on *Aplanes*.

Saprolegnia xylophila Kütz. ('43). As various members of this family grow readily on decaying wood in water, it is probable that this name refers to some of them. As it antedates the discovery of the sexual organs, Kützing's figure shows only the zoösporic stage, and the name cannot be referred to the synonymy of any particular species.

Saprolegnia corcagiensis Hartog ('87) is said to have the constrictions and zoösporangia of *Leptomitus lacteus*, and oögonia with pitted walls ("fenestratis"). It has been recognized only by Hartog and needs to be more completely characterized and further investigated.

Saprolegnia quisquiliarum Roumeg. ('91) has not to my knowledge been fully described, but is based on specimens issued as No. 5932 of the "Fungi Gallici." An examination of one of the specimens issued, made partly by my friend, Mr. A. B. Seymour, and partly by myself through his kindness, failed to discover anything Saprolegniaceous.

SPECIES EXCLUDENDÆ.

Saprolegnia minor Kütz. ('43) is probably an *Empusa*.

Saprolegnia DeBaryi Walz ('70) is probably a species of *Pythium*.

Saprolegnia siliquæformis Reinsch ('78) is *Monoblepharis prolifera* Cornu, according to Cornu ('77).

Saprolegnia Schachtii Frank ('81) is probably also a *Pythium*.

Saprolegnia Libertæ (Bory) Ktz. ('49) and three other names published by Kützing at the same time, viz., *S. candida*, *S. tenuis* and *S. saccata*, are followed by descriptions so imperfect as to have no individuality and no value.

Saprolegnia mucophaga Smith (Gard. Chron., XX, 781; 1883) and

Saprolegnia philomukes Smith (Gard. Chron., XXII, 245; 1884) do not belong to this family. They may be forms of *Pythium*.

Leptolegnia DeBary ('88).

Differs from *Saprolegnia* in that the oögonium contains a single oöspore which completely fills it.

Leptolegnia caudata DeBary ('88).

Ill.: DeBary, '88, Pl. IX, Fig. 5.

The single known species of this genus has narrow sporangia, ovate oögonia on short racemose branches, and antheridia, usually one to each oögonium, on branches of diclinous origin. It was obtained by DeBary from two different cultures from German mountain lakes, and is known only from these.

Pythiopsis DeBary ('88).

Hyphæ slender, much branched. Zoösporangia formed from their tips, globular, oval, ovate, or short-clavate, the later ones arising by cymose branching of the hyphæ, either sessile or on long branches. Zoöspores ovate, apically biciliate, escaping by a usually terminal mouth at the apex of a distinct papilla, and swarming separately; after encystment germinating without a second swarming stage, *i. e.*, monoplanetic. Oögonia and antheridia abundantly developed.

PYTHIOPSIS CYMOSA DeBary ('88).

Ill.: DeBary, '88, Pl. IX, Fig. 1.

Pl. XVII, Fig. 60-68.

Hyphæ slender, short. Zoösporangia from globular to short-clavate. Oögonia commonly terminal and globular, their walls unpitted, sometimes with a very few blunt outgrowths. Antheridia clavate, one, or rarely more, on each oögonium, usually arising just below its basal wall, rarely of diclinous origin. Oöspores single, or very rarely two, in the oögonium, excentric, with several oil-globules, their average diameter about 18 μ .

Massachusetts—Amherst. Europe.

The present interesting species, previously known only from DeBary's account, and obtained by him from a snow-water pool in the Vosges mountains, appeared in two of my cultures in March, 1892. Both were obtained from Algæ consisting chiefly of *Spirogyra* sp. One, from a ditch, had been kept in a jar in the laboratory since the preceding November, and had yielded *A. apiculata*, *Aph. scaber*, and *Dic-*

tyuchus sp. The other was freshly collected and gave also *A. cornuta*, *A. megasperma*, and *S. torulosa*.

I have not followed the zoöspore from its encystment to its germination; but, as the spores germinate freely in cultures which contain no trace of empty membranes, such as are seen with germinating diplanetie spores, there can be no doubt of their monoplanetism. The general appearance of the plant and of its sporangia strongly suggests a *Pythium*, as intimated in the generic name. The formation of the zoöspores does not appear to follow the course above described as characteristic of the family. I have not been able to study the process in detail, but it seems to be much simpler than that usual among *Saprolegniaceæ*. While the escape-papilla may appear more than three hours before the exit of the spores, no change is evident in the protoplasm of the sporangium until fifteen or twenty minutes before that event. The separation of the spores within the sporangium is very slight and I have seen nothing corresponding to the two separation stages, with an intermediate stage of swelling up. One might regard this as leading towards the simpler zoöspore formation of the *Peronosporæ*, but for the fact that the zoöspores are terminally, and not laterally, biciliate. The whole question deserves careful comparative study.

The outgrowths of the oögonial wall are only exceptionally rather long; and in the great majority of cases are not at all developed. In a very large number of oögonia examined, I have seen only one (Fig. 67) with more than a single oöspore. DeBary states that three sometimes occur. He also mentions the presence of as many as four antheridia on an oögonium. Amherst specimens have rarely had more than one each and never more than two. I have seen, also, the peculiar hyaline outer layer surrounding some oögonia, which was mentioned by DeBary; but cannot regard it as due to an extrusion of periplasm, as is suggested in his account ('88), since no periplasm is observed in other oögonia, and because it may occur on young oögonia before the formation of the oösphere, as well as on adult ones. I am, however, quite unable to explain its origin. On young oögonia it appears to be thicker than on older ones, but it has been seen at all in my cultures only exceptionally.

Achlya Nees ab Esenb. ('23).

Syn.: *Byssus aquatica* Fl. Dan. (1780).

Vaucheria aquatica Lyngb. ('19).

Hydronema Carus ('23).

Leptomitus prolifer Ag. ('24).

Saprolegnia capitulifera Braun ('51).

Exsic.: Algues de la France, 238 (*A. prolifera*).

Rabh., Algen Sachsens, 242 (*do.*).

Hyphæ usually stout, sometimes slender. Zoösporangia formed from their

swollen apices, usually thickest near the middle, *i. e.*, fusiform; the later ones arising on lateral branches from below the basal walls of the earlier ones, their successive formation resulting in a sympodial thread with apparently lateral sporangia. Zoöspores ovate or pyriform, at least sometimes, and probably always, apically biciliate, escaping by a single, usually terminal, mouth formed at the apex of a distinct papilla, and immediately becoming encysted and aggregated into a hollow sphere; after resting, swarming a second time in the laterally biciliate form; finally encysting again and germinating. Oögonia terminal or intercalary, one- to many-spored. Antheridia seldom wholly absent, often always present.

Key to recognized Species.

- | | | |
|-----------|--|--|
| <i>a.</i> | Oögonia with pitted walls..... | <i>b.</i> |
| | Oögonial walls not pitted..... | <i>c.</i> |
| <i>b.</i> | Plants diclinous..... | <i>A. prolifera.</i> |
| | Plants androgynous..... | <i>A. AMERICANA.</i> |
| <i>c.</i> | Oögonia with smooth walls..... | <i>d.</i> |
| | Oögonia with spiny walls..... | <i>i.</i> |
| <i>d.</i> | Plants strictly diclinous..... | <i>A. OBLONGATA.</i> |
| | Plants at least partly androgynous..... | <i>e.</i> |
| <i>e.</i> | Oöspores averaging ten or more..... | <i>f.</i> |
| | Oöspores averaging five or less..... | <i>g.</i> |
| <i>f.</i> | Oögonial branches short; oöspores excentric..... | <i>A. DeBaryana.</i> |
| | Oögonial branches long; oöspores centric..... | <i>A. POLYANDRA.</i> |
| <i>g.</i> | Oöspores over 40 μ in diameter; antheridial branches much branched..... | <i>A. MEGASPERMA.</i> |
| | Oöspores less than 40 μ in diameter; antheridial branches rarely branched..... | <i>h.</i> |
| <i>h.</i> | Oögonia usually apiculate; antheridial branches oftenest from the main hypha..... | <i>A. APICULATA.</i> |
| | Oögonia not apiculate; antheridial branches always from the oögonial branches..... | <i>A. RACEMOSA.</i> |
| <i>i.</i> | Antheridia on at least some oögonia..... | <i>k.</i> |
| | Antheridia wholly absent..... | <i>o.</i> |
| <i>k.</i> | Oögonia usually lateral at the ends of recurved branches..... | <i>A. recurva.</i> |
| | Oögonia terminal or intercalary, on straight branches..... | <i>l.</i> |
| <i>l.</i> | Oögonia globular; antheridia on each one..... | <i>m.</i> |
| | Oögonia oftenest elliptical; antheridia not on all..... | <i>n.</i> |
| <i>m.</i> | Oöspores averaging less than five; antheridial branches very short..... | <i>A. RACEMOSA</i> var. <i>STELLIGERA.</i> |
| | Oöspores averaging more than five; antheridial branches long..... | <i>A. oligacantha.</i> |
| <i>n.</i> | Oöspores 3-12, always globular..... | <i>A. PAPILLOSA.</i> |
| | Oöspores 1-3, often elongate..... | <i>A. spinosa.</i> |
| <i>o.</i> | Oögonia with rather sharp spines; oöspore single..... | <i>A. stellata.</i> |
| | Oögonia with blunt spines; oöspores one to three..... | <i>A. CORNUTA.</i> |

Achlya prolifera (Nees ab E.) DeBary ('52).

Ill.: DeBary, '52, Pl. VII, Figs. 1-28.

DeBary, '81, Pl. II, Figs. 1, 2, and IV, 1-4.

This is the commonest European species, but it is doubtful if it has been seen in this country. Either it or the almost equally common *A. DeBaryana* appears very frequently in cultures, there. It is clearly distinguished by the abundantly pitted walls of its oogonia, which resemble those of the next species, and by its numerous and long antheridial branches of declinous origin. Fungi reported under this name in American catalogues have belonged probably to the next or to other species.

From the fact of its abundance this species is rather more likely than any other to have been the one which Nees studied and called *A. prolifera*, although we have no means of knowing if this is actually the case. Under these circumstances there was no obligation to continue the name, but DeBary has chosen to do so by restricting it to this species; and, since it is the first name applied to the species, definitely recognized as such, and has been applied to no other recognizable species, it must stand. It is true that DeBary did not clearly characterize the species in the modern sense until 1881; yet in his earlier paper ('52) he described the pitted — or, as he then thought, perforated — walls of the oogonium; and as this is the only known European *Achlya* of that character, his description sufficiently marks the species, and the earlier date should be quoted for it.

ACHLYA AMERICANA sp. nov.

Ill.: Pl. XVIII, Figs. 69-73 (also on Pls. XIV-XVI).

Hyphæ stout, not very long. Zoösporangia very abundant, rather short and thick, slightly fusiform. Oögonial branches short, erect, racemosely arranged on the hyphæ. Oögonia terminal and globular, or rarely intercalary, their walls much pitted. Antheridial branches numerous, branching, arising from the main hyphæ between and near the oögonial branches. Antheridia very numerous, cylindric or somewhat clavate. Oöspores from one to fifteen in an oögonium, usually five to nine, excentric, their average diameter about 22 μ .

Massachusetts—Amherst: Pennsylvania—Philadelphia, *Keller*: Alabama—Auburn, *Atkinson*: Louisiana—St. Martinville, *Langlois*.

It is rather remarkable that our most abundant member of this genus, and indeed

of this family, so far as the writer's observations go, while closely resembling the two commonest European species, combines their characters in a peculiar manner. Like *A. prolifera*, our form has oögonia with abundantly and invariably pitted walls; but, like *A. DeBaryana*, its antheridial branches are of androgynous origin; and, like both, its oöspores are of excentric structure. The pits of the oögonial walls are not conspicuous as in the *Saprolegniæ* of the *ferax* group, although they are usually of considerable size; but treatment with the chloriodide of zinc always brings them out, as numerous transparent areas in the elsewhere deeply colored membrane. The antheridial branches are not so long nor so luxuriant as those of *A. DeBaryana*, as figured by DeBary ('81). They usually arise quite near the oögonial branches, very rarely even from the latter, which is said by DeBary never to happen in the last-named species; and the antheridia are rather shorter and envelop the oögonia less than is the case with the other.

These rather slight, but very constant, differences seemed at first to invalidate the distinction between the species called by DeBary *A. prolifera* and *A. polyandra*, and to indicate that they, with the present, are forms of a single variable species. But the very positive statement of so reliable an observer as DeBary as to the constancy of the characters of his two forms,* and the abundant evidence of repeated cultures from widely separated sources of the fixity of the present one, have left no alternative but to consider the three as distinct, though closely related, species, forming a series whose middle member is our American representative, and which may be termed the *prolifera* group.

I have met with this species in no less than twenty cultures from clean waters of every description, and from various parts of the country. It is the form referred to by the writer in an earlier note ('91) as "a form related closely to *A. polyandra* (perhaps that species);" and is that in which I first convinced myself of the presence of cilia on the escaping zoöspores of *Achlya*.

Achlya DeBaryana nom. nov.

Syn. : *A. polyandra* DeBary ('81).

Ill. : DeBary, '81, Pl. IV, Figs. 5-12.

Ward, '83, Pl. XXII, Figs. 1-14.

This is, as already stated, one of the commonest European species, but it has not been recognized in America. It has smooth, unpitted oögonia and long, branched

* I am indebted to Prof. Alfred Fischer, of Leipzig, who has had the opportunity of studying DeBary's material, for a full confirmation of that author's statements concerning these species.

antheridial filaments of androgynous origin, but agrees very closely in other respects with the two preceding species. As above indicated, it is the *A. polyandra* of DeBary, but it is clearly not the species to which that name was given earlier by Hildebrand ('67). DeBary appears to have believed that his species was that intended by Hildebrand; but, as will be fully shown later, this is not the case. And, since Hildebrand's species was pretty carefully described, it is perfectly recognizable. Hence the name *A. polyandra* belongs to it alone, and DeBary's species is left without a name. I therefore propose for the latter the name *A. DeBaryana*, in honor of the profoundest student of the *Saprolegniaceæ*, to whom so large a part of our knowledge of the family is due.

ACHLYA MEGASPERMA sp. nov.

Ill.: Pl. XVIII, Figs. 74-77.

Hyphæ stout, long. Zoösporangia thick, fusiform, freely developed. Oögonial branches short and straight, racemously arranged. Oögonia terminal, globular, with smooth and unpitted walls which are strongly thickened. Antheridial branches often arising near the oögonial branches, but apparently never from them, much branched, often producing no antheridia. The latter absent from many oögonia, from one to several on others, short-clavate. Oöspores two to eight, commonly four to six, in an oögonium, centric, very dark when young, their average diameter 45μ .

Massachusetts—Amherst.

Cultures from *Spirogyra*, dead leaves, etc., taken from a boggy spot by a small brook, are the only ones which have yielded the present well-marked species. The sporangia recall, in form and abundance, those of *A. Americana*, but the hyphæ are rather stouter and more vigorous than in that species. The very thick-walled oögonia, often without antheridia, and the very large oöspores, the largest known in this family, sometimes exceeding 50μ in diameter, distinguish it clearly from any other form. The thickening of the oögonial wall is not perfectly even, but its inner surface is somewhat irregular (Fig. 77) from unequal deposits of material. The protoplasm of the young oögonia and the oöspheres formed from it is very dense and dark colored, surpassing in this respect even that of *A. apiculata*. The plant is androgynous, but many of the smaller branches, which resemble in every other respect antheridial branches and strikingly suggest those of *A. DeBaryana*, fail to develop antheridia, and remain unattached to oögonia. Branches which do bear

antheridia are otherwise similar to these. The antheridia which attach themselves to a given oögonium may or may not arise from the same hypha with it, though such is perhaps more often the case.

The precise systematic position of the species is perhaps open to discussion, but it presents points of resemblance and probable relationship with both the last and the following species.

ACHLYA POLYANDRA Hildeb. ('67).

Syn. : *A. gracilipes* DeBary ('88).

Ill.: Hildebrand, '67, Pl. XVI, Figs. 7-11.

DeBary, '88, Pl. X, Figs. 2 and 6.

Pl. XVIII, Figs. 78-81.

Hyphæ stout, long. Zoösporangia often not abundant, secondary ones rare, nearly cylindrical. Oögonial branches usually very long and often recurved at the tip, racemose. Oögonia terminal, globular, with smooth and unpitted walls. Antheridial branches arising chiefly from the oögonial branches not far from the oögonia, often branched. Antheridia one to several on each oögonium, short-clavate. Oöspores five to twenty-five, usually ten to fifteen, in an oögonium, centric, their average diameter 27μ .

Massachusetts—Amherst. Europe.

First obtained in spring from Algæ from a temporary rain-pool in a depression in a grassy field, this species appeared later in a culture from *Confervæ* and *Vau-cheriæ*, taken from a running brook. Its numerous oöspores, very long oögonial branches, usually recurved at their tips, with the branched antheridial threads arising from them and bearing small and short antheridia, distinguish it from related forms. It appears to be rare with us, as I have never seen it from any other locality than Amherst, and only twice there.

It is especially interesting as having been the subject of a misunderstanding which has led to a confusion in synonymy that I have here attempted to correct. It was undoubtedly this species which Hildebrand described ('67) as *A. polyandra*. As has been already pointed out, DeBary gave the same name ('81) to a distinct species which he recognized as differing from Hildebrand's description, but thought to be probably his species. At the time of the completion of the paper quoted, DeBary had probably never seen this form, as his later paper ('88) states that he first obtained it in January of 1881, the year of the publication of the earlier one.

And while he did study it, he failed to notice its correspondence with Hildebrand's figures and description, and therefore named it anew *A. gracilipes*. But no one who will carefully compare the figures given by both authors will, I think, seriously question that they represent the same species. Again, Hildebrand states that secondary sporangia are not produced in his *A. polyandra*, a statement that DeBary ('81) disputes as untrue for his *A. polyandra*. But in his description of *A. gracilipes* ('88), DeBary says that secondary sporangia are only sparingly developed, a statement which I can corroborate for American specimens. The two descriptions agree in all other essential points, so far as they are comparable; and the evidence seems completely satisfactory that the correct synonymy of this distinct species is as above given.

The species shows as many points of affinity, perhaps, with *A. DeBaryana* and *A. megasperma* as with any others, but differs from them too widely to permit us to suppose any very recent common ancestry.

ACHLYA APICULATA DeBary ('88).

Ill.: Ward, '83, Pl. XXII, Figs. 15, 16.
DeBary, '88, Pl. X, Figs. 3-5.
Pl. XIX, Figs. 82-86, and XV, 26, 27.

Hyphæ stout, often long. Zoösporangia fusiform, abundant. Oögonial branches somewhat elongate, usually hooked or recurved, racemose. Oögonia terminal, globular or oval, oftenest with a distinct apiculus, rarely intercalary, their walls smooth and unpitted. Antheridial branches rather stout, mostly unbranched, from near the base of the oögonial branch, or sometimes from that branch. Antheridia one to several on each oögonium, short-clavate. Oöspores one to ten, commonly three to five, in an oögonium, centric, their average diameter about 36μ .

Massachusetts—Amherst: Alabama—Auburn, *Atkinson*. Europe.

So far as Amherst is concerned, this species is the most abundant after *A. Americana*. It has appeared in several cultures from various pools and ditches, and is not to be confounded with any other species. Its sporangia are often more strikingly fusiform than those of most *Achlyæ*, as is well shown in Ward's figures ('83) and in our Fig. 82. The apiculate oögonia which contain, when young, a very opaque, dark-colored protoplasm, and, when old, a few large oöspores, are very characteristic and easily recognized. The oöspores are surpassed in size and opacity

only by those of *A. megasperma*, and may reach, in extreme cases, a diameter of rather more than 40μ . I have not observed the tendency towards the excentric type of oöspore said by DeBary to be sometimes shown by this species in the one-sided position of the oil-globule.

This plant shows some striking affinities with *A. megasperma* and *A. polyandra*; and, while in some respects intermediate between them, seems to take the position here given it with less violence to all considerations.

ACHLYA OBLONGATA DeBary ('88).

Ill. : DeBary, '88, Pl. X, Figs. 7-9.

Pl. XIX, Figs. 87-89.

Hyphæ stout. Zoösporangia slightly fusiform, not abundant. Oögonial branches short or rarely somewhat elongate, straight, racemosely arranged. Oögonia occasionally intercalary, usually terminal, and elliptical, ovate, or obovate, rarely globular, with smooth, unpitted walls. Antheridial branches slender, of strictly diclinous origin, sometimes branched. Antheridia on every oögonium, numerous and small, short-clavate. Oöspores from one to twenty, usually seven to nine, in an oögonium, centric, their average diameter about 27μ .

Massachusetts—Amherst: Louisiana—St. Martinville and Bayou Tortue, *Langlois*. Europe.

The elongate oögonia and diclinous hyphæ readily separate this type from all other *Achlyæ*, no other diclinous species being known except *A. prolifera*. It has occurred in cultures from Mill river, in Amherst, and from the aquatic room of the Plant-house of the Massachusetts Agricultural College, as well as in two cultures from Louisiana. The oögonia, which are typically rounded at their apices, show a tendency to a pointed form in some Louisiana specimens (Fig. 88); while in all cultures some of them are of a distinctly globular form, especially such as terminate principal hyphæ.

The oöspores commonly do not occupy the whole interior of the oögonium, but are collected into a group at one side, leaving an empty space. I do not, however, find them "viel kleiner als die aller Verwandten," as they are said by DeBary ('88) to be.

In the form and size of its antheridia and the delicacy of its antheridial branches as well as in its strict dicliny, the species strongly recalls *S. diclina*, but the resemblance goes no further.

Var. GLOBOSA var. nov.

III. Pl. XIX, Figs. 90, 91.

Oögonial branches very short; oögonia globular; oöspores reaching twenty-five in number, averaging ten to fifteen; otherwise as in the type.

Pennsylvania—Philadelphia, *Keller*: Alabama—Auburn, *Atkinson*.

While not sufficiently different to be considered specifically distinct, this is certainly a well-defined variety of *A. oblongata*, marked by the very constant distinctions above indicated. It has been received from two widely separated localities, and appears to remain constant in culture. The oögonia are commonly larger than in the type and the space unoccupied by spores is much more marked (Fig. 90), sometimes amounting to more than half of the cavity. The antheridia correspond completely with those of the type, and furnish the best grounds for regarding the differences as of only varietal value.

This species shows no marked affinity with any other single species of *Achlya*, and its insertion at any particular point in the series is comparatively arbitrary. No real indication of affinities is possible in a linear arrangement of these species.

ACHLYA RACEMOSA Hildeb. ('67).

Syn.: *A. lignicola* Hildeb. ('67).

III.: Hildebrand, '67, Pl. XV, Figs. 1-9, and XVI, 1-6a.
Cornu, '72, Pl. I, Figs. 2-8.
Pl. XIX, Figs. 92-95.

Hyphæ robust. Zoösporangia nearly cylindrical, sometimes tapering. Oögonial branches racemosely arranged, short and straight. Oögonia globular, their walls smooth and unpitted, somewhat irregularly thickened within, brownish-yellow when old. Antheridial branches very short and simple, arising from the oögonial branches near the basal walls of the oögonia, either above or below them. Antheridia one or two, rarely three or four, to each oögonium, short-clavate, usually bent, and applied by their apices to its wall. Oöspores one to ten, commonly two to six, in an oögonium, centric, their average diameter about 25 μ .

Massachusetts—Amherst. Europe.

The typical form of the species, which was studied by Hildebrand, has appeared in two cultures in Amherst, one from dead leaves and slime from the outlet of a

spring, and the other from a few *Ulothrichaceæ* taken from an open cask sunk in the soil of a pasture and apparently filled only by rains. It does not seem to be common. The species is readily recognized by the very characteristic antheridia, which are quite unlike those of any other species. The color of the old oögonial wall and its irregular thickening are also constant features. At the points of application of the antheridia hardly any secondary thickening occurs, so that it remains thin there.

There can be no doubt that Hildebrand's *A. lignicola* is merely a depauperate form of the present species, probably due in part to its growth on vegetable remains. There seems to be no reason for giving it even varietal rank. But we may distinguish clearly the

Var. *STELLIGERA* Cornu ('72).

Syn.: *A. racemosa* var. *spinosa* Cornu ('72).

A. colorata Pringsh. ('82).

Ill.: Hine, '78, Pl. VI, Figs. 1-14.

Pringsheim, '74, Pl. XIX, Figs. 1-15; XXI, 1-3, 13;
and XXII, 1-3.

Pringsheim, '82, Pl. XIV, Figs. 12, 15-31.

Pringsheim, '83b, Pl. VII, Figs. 10-20.

Pl. XIX, Figs. 96-98.

Oögonial walls more or less abundantly producing short, rounded outgrowths, more deeply colored when old. Oöspores very rarely exceeding five in an oögonium. Otherwise as in the type.

Massachusetts—Amherst and Northampton: New Jersey—Glassboro', *Keller*: New York—Ithaca, *Hine*: Louisiana—Bayou Tortue, *Langlois*. Europe.

This form seems much more abundant with us than the type. It was first recorded as American by Hine ('78); for although it was not definitely identified by him, his figures are unmistakable. I have observed it in cultures from three different sources in Amherst and its vicinity, including a swamp pool, a fish hatchery, and a river; also from a cedar swamp in New Jersey and from a Louisiana bayou. Though the degree of development of the spines may vary considerably in different specimens from the same culture, I have never seen a wholly smooth oögonium in a culture of the spiny form, or a spiny one among those of the typical form. And it is this fact which has seemed to indicate the propriety of characterizing the spiny form as a distinct variety. The two spiny varieties named by Cornu ('72) are apparently based on specimens with the spines respectively more and less developed; and, in the absence of evidence to the contrary, must be regarded as representing extremes

of development within the limits of a single variety. The name *STELLIGERA* has been chosen of the two used by Cornu, to avoid confusion with *A. spinosa* DeBary, which is a very distinct species, in spite of the fact that it is quoted in Saccardo's *Sylloge* ('88) as a synonym of *A. racemosa* var. *spinosa* Cornu.

Besides the spiny oögonia and the fewer oöspores, one observes that in this variety the antheridial branches are, on the whole, even shorter than in the type-form, and more frequently arise from the wall of the oögonium itself than in the latter.

In February, 1891, I received, through Dr. J. B. Paige, of the Massachusetts Agricultural College, some trout eggs from the Northampton fish hatchery, which were evidently attacked by a fungus of this family, and were dead. The hyphæ failed to develop sexual organs, but fresh cultures, obtained by throwing flies into the vessel containing them, produced a new crop, bearing the sexual organs of this form. I was unable to visit the hatchery, but am informed that it proves necessary to remove dead eggs very frequently, since the infection spreads rapidly, and all the eggs in the hatching trays are killed unless this is done. After the eggs are hatched, the young fry appear not to be injured by the fungus. If this be true, the present species would seem to possess less parasitic capacity than the fungus of the salmon disease. It is probable that, in case of the eggs, the fungus can attack only the non-living egg-membranes, and that the death of the living cells of the egg is an indirect and not a direct result of its attack.

This variety may represent a transitional form between some smooth and spiny species of *Achlya*, not only as regards their oögonial structure, but also in the reduction of the antheridial branches, which is carried even to their entire disappearance in some spiny species.

Achlya oligacantha DeBary ('88).

Ill. : DeBary, '88, Pl. X, Fig. 1.

The present species has delicate hyphæ which bear globular oögonia with rather few spines, and commonly four to eight oöspores each. Antheridia are developed on all the oögonia from rather elongate, simple branches of androgynous or diclinous origin. It has been observed by DeBary in a single culture from Baden, but not yet elsewhere. It may be regarded as representing a spiny form of the *polyandra* type, and in this respect differs from the spiny species to be described, which do not resemble closely any of the smooth-walled species, but constitute a distinct group of forms.

ACHLYA PAPILLOSA sp. nov.

Ill.: Pl. XX, Figs. 99-102.

Hyphæ rather slender, long. Zoösporangia sparingly developed, cylindrical, little larger than the hyphæ. Oögonia terminal on main threads or on short lateral branches, or sometimes intercalary, oval or ovate, rarely globular, thickly studded with short, blunt, wart-like outgrowths of their unpitted walls, often with a marked apiculus. Antheridial branches usually developed with each oögonium, fine and branching, arising near it from the main thread, or rarely from the oögonial branch. Antheridia imperfectly formed. Oöspores as many as twelve in an oögonium, oftenest four to six, centric, their average diameter about 25μ .

Massachusetts—Amherst.

This plant, which seems to be sufficiently distinct from previously described species, has been obtained in several cultures, but from only a single source; namely, the very prolific mossy pool in Amherst, already mentioned. It may be recognized by its long hyphæ, finer than those of most *Achlyæ*, and its oögonia with warty, rather than spiny, walls, and several oöspores in each. I have never seen well-differentiated antheridia or fertilization-tubes, although the ends of the antheridial branches are applied to the oögonia.

While bearing no near resemblance to any species heretofore figured, this plant may be somewhat closely related to the next, if the latter is well founded.

Achlya recurva Cornu ('72).

So far as the incomplete account published by its author enables one to judge, this is a distinct species from the last, and is separated by its longer and recurved oögonial branches, on which the oögonia are usually borne laterally, and by its better developed antheridia, often digitately branched. Aside from the original observations of its author ('72), this species has been recognized only by Hartog ('88).

Achlya spinosa DeBary ('81).

Ill.: DeBary, '81, Pl. IV, Figs. 13-18.

Its author's latest description of this species ('88) does not fully agree with his earlier figures ('81), especially in that he states that the oögonia are never intercalary,

while he has figured several such. It should be, however, readily enough recognized by the usually barrel-shaped oögonia, with numerous blunt, and often broad or even forked, outgrowths, each containing one or two oöspores which often take an elliptical form corresponding to that of the cavity of the oögonium. The principal hyphæ commonly produce very abundant closely set, short, lateral branches that give to the whole plant a densely woolly appearance; and reproductive organs are often produced only when these branches reach a new food-supply and give rise to fruiting hyphæ. The species was obtained by DeBary from a lake in the Black Forest, known as the "Titisee."

ACHLYA CORNUTA Archer ('67).

Ill.: Archer, '67, Pl. VI, Figs. 2-6.

Pl. XX, Figs. 103, 104.

Hyphæ of medium size, short. Zoösporangia rare, cylindric. Oögonial branches rarely long, straight or flexuous, racemosely arranged. Oögonia terminal, globular or elliptical, densely beset with rather long, blunt outgrowths of their unpitted walls, the apical one often larger and forming an evident apiculus. Antheridial branches and antheridia wanting. Oöspores from one to four in an oögonium, globular or slightly flattened, centric, their average diameter about 29μ .

Massachusetts—Amherst. Europe.

The same culture which yielded *A. megasperma* for the first time contained a small amount, all I have seen, of this form. It has been referred with some doubt to Archer's species, since it fails to show at all a feature which one would suppose, from that author's account and figures, to be very characteristic of his plant; namely, the development of several oögonia in a series from a single hypha. In other respects, however, it corresponds too closely with his description to justify one in regarding it as distinct. Archer saw no sporangia, probably not, as he thought, because he found it too late, but because of their rarity. In species which produce sporangia abundantly, one can always find empty ones on plants with mature oöspores. In the limited material at my disposal, I have been able to find but a single one, and that only long after it was emptied. From below its base arose a branch bearing an oögonium. This, so far as it goes, supports Archer's conclusion that the plant is an *Achlya*, which seems almost certainly correct. The oögonial branches sometimes show the incurving mentioned by Archer, and are often less definitely bent. This writer states

that an oogonium may contain as many as eight or ten oöspores; but I have never seen more than four, and his figures show no more than three. He describes no special antheridial branches, but says that the antheridia are like those of *A. dioica* Pringsh. As these latter are not antheridia at all, one would expect to find, as is the case with American specimens, that the species has no true male organs. As will be seen from the figures, the spines could hardly be more closely set, and their form is more cylindrical than conical.

This and the next species seem to be closely related, the more so if the American form here described proves to be more typical than Archer's.

Achlya stellata DeBary ('88).

Ill.: DeBary, '88, Pl.X, Figs. 10, 11.

Like the last, to which, indeed, it seems almost too similar, this plant has no antheridia. Its globular or elliptical oogonia are covered by rather less numerous spines that are shorter and sharper, therefore more conical, than those of *A. cornuta*. The oöspores are always single and sometimes correspond in form with the cavity of the oogonium, instead of being always globular. It is known only from a single locality near Göttingen.

SPECIES INQUIRENDÆ.

Achlya contorta Cornu ('72, Pl. I, Figs. 9-15), with smooth oogonia, containing on an average eight oöspores, and borne on long, spirally twisted branches with peculiar local swellings, and with branched cylindrical antheridia; and *Achlya leucosperma* Cornu ('72), with antheridia similar to the last, and oogonia with two-pitted walls and light-colored oöspores, have been studied only by their author, whose descriptions are too imperfect to determine their position. While they may prove to be distinct species, more definite and complete information concerning them is much needed.

Achlya dioica Pringsh. ('60, Pl. XXIII, Figs. 1-5), should be written as a synonym, probably of some species already described; but as the oogonia were not mentioned or figured, it is impossible to say to what species it belongs. The name was given to some hyphæ said by the author to be those of an *Achlya*, which were attacked by a Chytridiaceous parasite, probably that since described by Cornu ('72)

as *Woronina*. The cysts of the parasite were supposed to be the antheridia of the fungus. This belief, which also led to the similarly erroneous application of the name *Saprolegnia dioica*, was based on the supposed necessity for the existence of antheridia and a sexual process in these plants.

Achlya Nowickii Racib. (Przyrodnik [The Naturalist] V, 327; 1884) may be a good species, but I have not been able to examine the original description.

Achlya penetrans Duncan (Proc. Roy. Soc. London, XXV, 238; 1876) is probably a boring Siphonaceous alga.

Aphanomyces DeBary ('60).

Hyphæ very slender and delicate, little branched, forming a nebulous film over the substratum. Zoösporangia formed from their unswollen ends, often a hundred or more times as long as broad; secondary ones not abundant, formed by cymose branching. Zoöspores cylindric-fusiform, cilia not yet observed, formed in a single file in the sporangium, and escaping slowly by a terminal mouth which is formed without the preliminary development of an oral papilla; immediately becoming encysted and aggregated into a hollow rounded group; after resting, swarming in the laterally biciliate form; finally encysting again and germinating. Oögonia usually terminal and one-spored. Antheridia commonly present.

Key to established species.

- a. Parasitic on *Zygnemaceæ*; oögonia spiny.....*Aph. phycophilus*.
Saprophytic.....b.
- b. Oögonia quite smooth; antheridia always present.....*APH. LÆVIS*.
Oögonia roughened or spiny.....c.
- c. Spines large and prominent; antheridia always present.....*Aph. stellatus*.
Spines small or reduced to mere roughnesses; antheridia often absent.....*APH. SCABER*.

APHANOMYCES LÆVIS DeBary ('60).

Ill.: DeBary, '60, Pl. XX, Figs. 17, 18.

Pl. XX, Figs. 105-107.

Zoösporangia very long and slender. Oögonia terminal on short lateral branches, globular, with entirely smooth walls. Antheridia abundantly developed on all

oögonia, large, clavate-cylindric, on short branches of androgynous or diclinous origin, sometimes even from the oögonial branch. Oöspores single, globular, centric, 20 to 22 μ in diameter.

Massachusetts—Amherst. Europe.

The present species appeared in a single culture from moss and Algæ (chiefly *Tolypothrix*) from the mossy pool frequently mentioned, which had stood in a jar in the laboratory for several months. It is readily distinguished by its smooth oögonia from all other species except the smoothest forms of *Aph. scaber*, from which it differs in its large and numerous antheridia and larger oöspores. The fertilization tubes are plainly developed and the species seems in all respects to represent the most primitive form of the genus.

It is worthy of remark that, although the genus was described more than thirty years ago, no other species than the four then characterized have yet been recognized.

Aphanomyces stellatus DeBary ('60).

Ill.: DeBary, '60, Pl. XIX, Figs. 1-13.

Sorokine, '76, Pl. VII.

Distinctly marked by its oögonia with large, blunt spines or warts, and its well-developed antheridia, which seem to be present on every oögonium, combined with its strictly saprophytic habit. DeBary states that in rare cases an oögonium may contain two oöspores, the only deviation from the one-spored condition known to occur in the genus.

This species has been studied by Sorokine ('76), as well as by its author, and is probably common in Europe, and perhaps also in America, though I have not yet met with it. It seems to be similar to the last species except in the spiny character of its oögonia, a condition towards which, whatever its significance, there is a distinct tendency in several groups of species in this family.

Aphanomyces phycophilus DeBary ('60).

Ill.: DeBary, '60, Pl. XX, Figs. 19-24.

Although the zoösporangia and sexual organs were not observed by DeBary on the same plant, there seems to be little doubt that this species is properly placed

in the present genus. Its oögonia are the largest of the genus and have relatively smaller and sharper spines than the last species, while its antheridia are well developed and always present. But its chief peculiarity lies in its parasitism upon Algæ, in which it is unique among *Saprolegniaceæ* and recalls the related genus *Pythium*. Its host-plants are *Spirogyra* and *Zygnema*, whose cells it rapidly destroys. It has been observed as yet only in Europe. While structurally distinct from the last species, and shown by DeBary to be also physiologically so, this must be regarded as a plant of the same type, which has acquired the parasitic habit.

APHANOMYCES SCABER DeBary ('60).

Ill. : DeBary, '60, Pl. XX, Figs. 14-16.

DeBary, '81, Pl. VI, Figs. 30-36.

Pl. XX, Figs. 108-111.

Zoösporangia very long. Oögonia small, terminal on short branches, or on main hyphæ, globular; their walls with numerous short spines or prominences, or merely irregularly roughened. Antheridia on branches of androgynous or diclinous origin, small, not on all oögonia. Oöspores single, globular, centric, 16 to 18 μ in diameter.

Massachusetts—Amherst. Europe.

The spiny form of this species (Figs. 108, 109) appeared in a single culture from dead leaves and slime taken from a ditch in Amherst, and the merely rough form (Figs. 110, 111) was obtained later from a mass of *Spirogyra* which grew in the same ditch, at a point a few rods away from the source of the first.

Both forms agree closely except in the roughnesses of the oögonia, which may be very slight or may take the form of short and rather sharp spines. But the species is always known by the smaller oöspores and by the reduced size and number of the antheridia. These latter are wholly wanting on half or even more of the oögonia. In my few cultures they have been rather less abundant in the smoother than in the spiny form, and the two extreme types of oögonia have not appeared together. It may therefore prove justifiable to regard the smoother form as a distinct variety, but further evidence is needed on this point. The character of the present species points to the conclusion that it should be regarded as the least typical of the genus, representing a degeneration in both sexual organs from the type of *A. stellatus*.

*Thraustotheca** gen. nov.

Hyphæ stout, branching. Zoösporangia formed from their swollen ends, clavate; the later ones formed by sympodial branching. Zoöspores encysting within the sporangium at once after their formation, somewhat polyhedral from pressure, but with distinct membranes; soon set free by the breaking up of the very fragile sporangial wall, and then escaping from their cysts to swarm in the laterally biciliate form; finally encysting again and germinating. Oögonia several spored, with abundant antheridia.

Thraustotheca clavata (DeBary).

Syn.: *Dictyuchus clavatus* DeBary ('88).

Ill.: Büsgen, '82, Pl. XII, Figs. 1-8.

DeBary, '88, Pl. IX, Fig. 3.

This, the only species of the genus yet known, strikingly resembles *Achlya DeBaryana* in its sexual organs, having similar long and branching antheridial threads and smooth oögonia with excentric oöspores. But its short, clavate sporangia and the peculiarities in the development of its zoöspores separate it widely from the latter. It is known only from near Strassburg, Germany.

A careful comparison of the characters of this species, as drawn from the accounts of Büsgen ('82) and DeBary ('88), with those of species of *Dictyuchus*, taken from the American specimens studied by the writer, will furnish, it is believed, sufficient justification for its separation from the latter genus. An account of the differences on which the new genus is based will also be found in the discussion of generic relationships on a previous page. The close analogy of the sporangia of this plant with those of *Mucor* has already been pointed out by Solms-Laubach, to whom we owe the arrangement of incomplete fragments of DeBary's last paper ('88), and he has also hinted at the possibility of generic differences between this and the other described species of *Dictyuchus*. His suspicions are quite supported by the very different means adopted, in the two types, for the release of the zoöspores after their encystment within the sporangium. The species needs further study, especially with reference to the nature of the intermediate substance said to exist between the zoöspores within the sporangium.

Dictyuchus Leitgeb ('68).

Hyphæ stout or slender, branching. Zoösporangia formed from their swollen ends, usually fusiform; the later ones formed in basipetal succession below the earlier,

* *θραυστός*, fragile; *θήκη*, a case.

or by sympodial branching, or in both ways on the same hypha. Zoöspores encysting within the sporangium at once after their formation, polyhedral from mutual pressure, the membrane of each face united with that with which it is in contact to form an apparently single wall; after a time escaping, each by a separate opening through the outer wall, and swarming in the laterally biciliate form; finally encysting again and germinating. Oögonia terminal or intercalary, one- or several-spored. Antheridia usually present.

Key to the known Species.

- a.* Plants diclinous; oöspores single.....*b.*
Plants androgynous; oögonia several-spored.....*D. polysporus.*
- b.* Oögonia under 30μ in diameter, encircled by the antheridia.....*D. monosporus.*
Oögonia over 30μ in diameter, not encircled by the antheridia.....*D. MAGNUSII.*

DICTYUCHUS MAGNUSII Lindst. ('72).

Ill.: Lindstedt, '72, Pl. I, Figs. 1-15.

Pl. XX. Figs, 112-114.

Hyphæ rather large. Zoösporangia cylindric or fusiform. Oögonia terminal on slender branches, globular, smooth-walled, unpitted. Antheridia cylindric or slightly clavate, on all oögonia, borne on slender branches of diclinous origin. Oöspores single, centric, about 25μ in diameter.

Massachusetts—Cambridge, *Trelease*. Europe.

Our knowledge of the occurrence of this species in America rests on the notes and preparations of Prof. *Trelease*, who obtained it in 1881 from water in the Botanic Garden, at Cambridge. It can be confounded only with *D. monosporus*, from which it differs in its somewhat larger oögonia and less coiled antheridial branches.

Lindstedt states that it is only in this species that the sporangia are formed from the hyphæ in basipetal succession, but it seems doubtful if this is strictly true, in view of certain observations to be mentioned later.

The definition of the present genus by its author was less restricted than that above adopted, which is essentially that of Lindstedt ('72), but seems, for reasons suggested in the discussion of the genus *Thraustotheca*, to be a more accurate and philosophical one.

Dictyuchus monosporus Leitgeb ('69).

Ill.: Leitgeb, '69, Pl. XXII, Figs. 1-12; XXIII, 1-8.

Not yet known in America. Resembles the last species closely, but has smaller oögonia and short, coiled antheridial branches.

Dictyuchus polysporus Lindst. ('72).

Ill.: Lindstedt, '72, Pl. II, Figs. 1-3; III, 1-7.

Distinguished by its large, globular, many-spored oögonia and its antheridial branches of androgynous origin, from all other described species of the genus. Not seen in America.

In one of my cultures of *Aph. scaber* there appeared hyphæ and sporangia of a species of *Dictyuchus*. A vigorous growth of it was readily obtained on fresh flies and kept up in successive generations for several months. In ordinary cultures in glass vessels, the sporangia are freely and normally produced both in basipetal series and by cymose branching. In cultures on slides in a moist chamber, one often sees sporangia lobed and forked in quite irregular fashion, like those figured by Leitgeb ('69) for *D. monosporus*. The plant seems slenderer and more delicate than *D. Magnusii* of Prof. Trelease's preparation, and is very probably not that species. It does not appear that either the basipetal development of sporangia or their forked shape can be regarded as of any specific value. In spite of repeated efforts to induce their development, the sexual organs of this plant have uniformly failed to appear, so that it is quite impossible to say what species it represents. After the formation of sporangia has begun to decline, the main hyphæ of a plant commonly send out a mass of fine lateral branches, themselves much branched and interlacing, which give to the whole culture a densely woolly appearance. These threads probably correspond to those which bear the sexual organs in *D. monosporus*, but, although readily kept alive and healthy for a long time, they remain persistently sterile. Gradually the later generations of the plant showed signs of degeneracy, and ultimately refused to yield normal plants.

Two or three cultures from various sources have produced a plant with slender hyphæ and sporangia of the *Dictyuchus* type, except that they contain only a single file of zoöspores, being cylindrical and little larger than the hyphæ. It is this form whose sporangium is shown in Fig. 16. I have never been able to find its sexual organs, and specific determination is, therefore, impossible.

Aplanes DeBary ('88).

This genus represents the extreme result of the reductional tendencies observed in previous genera, in that both swarming stages are entirely suppressed. The zoö-spores encyst within the sporangium and germinate there, producing germ-tubes which penetrate the sporangial wall and thus make their way into the surrounding water.

Aplanes androgynus (Archer).

Syn.: *Saprolegnia androgyna* Archer ('67).

Achlya Braunii Reinsch ('78).

Aplanes Braunii DeBary ('88).

Ill.: Archer, '67, Pl. VI, Fig. 1.

Reinsch, '78, Pl. XIV, Figs. 1-6.

DeBary, '88, Pl. IX, Fig. 2.

The present very striking species would seem not to be rare in Europe, having apparently been met with by several investigators; but it is not known to be American. It is recognized by its several spored, barrel-shaped or spindle-shaped oögonia, with pitted walls, often formed in series from a hypha, and by its numerous antheridial branches arising just below the basal wall of each oögonium, even though it be from the sides of the next oögonium in the series.

Although it is not absolutely certain that the plants studied by Archer, Reinsch, and DeBary all belonged to the same species, there seems to be little doubt of the correctness of such a conclusion, in spite of the fact that Reinsch's account of the sporangia does not agree with DeBary's, and that Archer does not mention the pits of the oögonial wall. The overlooking of the latter would have been less remarkable twenty-five years ago than to-day; and Archer's failure to see the sporangia is readily explained by DeBary's statement that they are very rarely developed. Archer's arguments for placing his plant in the genus *Saprolegnia* are drawn wholly from analogy, and not from observation of the sporangia.

Reinsch's description of the sporangia suggests that he perhaps did not see those of the plant whose sexual organs he studied, but mistook for them those of a *Dictyuchus* which may have grown intermingled with the other. At all events, the agreement in the structure of the sexual organs has led DeBary to feel very sure of the identity of his plant with Reinsch's, but he seems to have overlooked the equally complete similarity of Archer's plant. It seems best, then, to consider all the names above quoted as synonyms; and, while retaining DeBary's generic name, the plant must bear the specific designation given it by Archer, since that is the older.

*Subfamily Leptomiteæ.***Leptomitus** Agardh ('24).Syn.: *Apodya* Cornu ('72).

Hyphæ stout at the base, marked off at intervals by deep constrictions into distinct segments; branching abundant, dichotomous below, but often monopodial on the finer ultimate divisions; branches arising only from the acroscopic ends of the segments. Zoösporangia formed from swollen segments of the hyphæ which are cut off at the constrictions; the primary ones from apical segments, and later ones often several in basipetal succession. Zoöspores biciliate, monoplanctic (?), swarming separately. Oögonia and antheridia unknown.

LEPTOMITUS LACTEUS (Roth) Ag. ('24).Syn.: *Conferva lactea* Roth (1789).*Saprolegnia lactea* Pringsh. ('60).*Apodya lactea* Cornu ('72).

Exsic.: Rabh., Algen Sachsens, 587.

Ill.: Dillwyn, '09, Pl.

Pringsheim, '60, Pl. XXIII, Figs. 6-10; XXV, 1-6.

Pringsheim, '83b, Pl. VII, Figs. 1-9.

Büsgen, '82, Pl. XII, Figs. 9-15.

Pl. XX, Figs. 115-118.

Hyphæ rapidly decreasing in diameter with successive subdivisions; apical segments about 10μ in diameter and often forty times as long. Zoösporangia cylindrical, from slightly swollen segments, their mouths terminal or lateral. Zoöspores in a single file within them.

Massachusetts—Amherst: Connecticut—Bridgeport, *Holden*. Europe. Probably common everywhere.

This unmistakable form appears to be common enough in Amherst, and is undoubtedly so elsewhere in favorable situations. It prefers, as has been before intimated, waters which are somewhat, but not too strongly, polluted by organic substances. I first met with it on masses of decaying Algæ which had died and broken down in the vessel in which they had been kept. Afterwards it appeared in fly cultures from waters from the outlets of drains, containing decaying vegetable matter. It does not appear to flourish where active decay of animal substances is going on. In favorable places, it often forms very dense masses of closely felted threads, covering very large surfaces. Göppert observed ('52) such a case in a small stream below a beet-molasses manufactory, near Schweidnitz, in Silesia. I

have received from the herbarium of Prof. W. G. Farlow a specimen from a similar mass, collected in a stream, below a "tripe-house," at Bridgeport, Conn., by Mr. Isaac Holden.

The species is easily recognized by the regularly dichotomous branching and rapid reduction in size of its principal hyphæ, and by its cylindrical sporangia developed in basipetal succession. While the zoöspores ordinarily escape from the sporangia, they sometimes become encysted within them (Fig. 117). It is this fact, probably, which led Braun to state ('51) that the spores of *Leptomitus* are arranged in a row in the spore cases, and that "no active gonidia seem to occur."

The hyphæ of this plant are especially favorable for the study of the so-called cellulose grains. Frequently, when a sporangium is formed, its narrow connection with the next segment is closed by the occupation of the passage by one of these granules. This simple method of forming a cross partition is perhaps not very different in kind from that which occurs in the *Saprolegniæ*.

SPECIES INQUIRENDÆ AUT EXCLUDENDÆ.

Many so-called species of this genus have been described by early authors, and may be found catalogued by Kützinger ('49), and in part by Saccardo ('88). The great body of them are merely sterile, submerged hyphæ of uncertain origin, and even to list them here would be useless. The only species which need be mentioned, and concerning which further information is desirable, are:

Leptomitus Libertii (Bory) Ag. ('24) [Exsic., Libert, Plantes Crypt. Ard., 97], placed doubtfully by Saccardo ('88) under *Saprolegnia*. The published description mentions no reproductive organs and I have not been able to examine Libert's *exsiccata*. So far as the description goes, the plant may belong to this family, but probably rather to the *Saprolegniæ* than to the present subfamily.

Leptomitus rubescens DeBréb. [Exsic., Algues de la France, 306], and

Leptomitus Doriæ Ces. [Exsic., Rabh., Algen Sachsens, 575] are mentioned only in the quoted *exsiccatæ*. They will probably prove to be only sterile hyphæ.

Apodachlya Pringsh. ('83b).

Hyphæ slender throughout, marked off at intervals by constrictions into distinct segments; branching monopodial; branches arising from any part of a segment.

Zoösporangia from considerably swollen segments, renewed by sympodial branching. Zoöspores usually becoming grouped at the mouth of the sporangium, on escaping, rarely swarming separately; soon leaving their cysts and swarming; finally encysting again and germinating. Sexual organs known in but one species.

As Pringsheim has observed in one species ('83b), and Zopf in another ('88), that the zoöspores commonly escape after the manner of *Achlya*, there seems to be as good reason for the generic separation of the following species from *Leptomitius*, as for keeping *Saprolegnia* and *Achlya* distinct, and also since there are marked differences in the branching of the hyphæ and in the formation of secondary sporangia.

The species heretofore recognized are:

Apododachlya brachynema (Hildeb.) Pringsh. ('83b).

Syn.: *Leptomitius brachynema* Hildeb. ('67).

Ill.: Hildebrand, '67, Pl. XVI, Figs. 12-23.

Has hyphæ with short segments, and globular sporangia opening by short necks and often occurring in series. No sexual organs are known.

Apodachlya pyriferæ Zopf ('88).

Ill.: Zopf, '88, Pl. XXI, Figs. 1-21.

Has hyphæ with long segments, pyriform sporangia, developed singly and each opening by a distinct papilla, and large globular chlamydospores. Sexual organs have not been seen.

To these species it seems necessary to add:

APODACHLYA (?) *COMPLETA* sp. nov.

Ill.: Pl. XX, Figs. 119-121.

Hyphæ slender, with rather long segments. Zoösporangia unknown. Oögonia terminal on branches of one or a few segments, each representing a swollen segment, globular, with smooth, unpitted walls. Antheridia formed from lateral cylindrical branches of one or two segments which arise from the slightly swollen apical part of the segment next below the oögonium, usually two from each. Oöspores oftenest five to seven, sometimes less or more, thick-walled when mature, centric, 18 to 20 μ in diameter.

Louisiana—St. Martinville, *Langlois*.

This very interesting plant affords the first recorded instance of the occurrence of sexual organs among the *Leptomitæ*, unless the imperfectly described *S. (Leptomitus) corcagiensis* of Hartog be such an example. The latter cannot, however, be the same form as the present one. This plant appeared in very limited quantity on a fly which had been thrown into an old and feeble culture of *Saprolegnia* sp., obtained by Rev. Mr. Langlois from a ditch in St. Martinville, La. The moribund condition of the culture when it was received caused these freshly added flies to decay so much that the development of other *Saprolegniæ* was slight and unhealthy; but the few plants of this form were developed normally and seemed to find their surroundings congenial, indicating that it, like *L. lacteus*, is partial to polluted waters.

A very careful and detailed examination of the material failed to discover any sporangia, and it does not, therefore, certainly belong to the present genus. But, since the hyphæ are certainly not those of *L. lacteus*, but are slender throughout, branch monopodially from all parts of their rather long segments, and in general resemble strikingly those of *Apod. pyriferæ*, it is placed provisionally here.

Its great interest lies, as before suggested, in its possession of well-formed sexual organs of peculiar and characteristic structure. The oögonia are globular and are formed by the swelling of the terminal segment of a branch. When young, they are filled by granular protoplasm which is entirely used up in the formation of the oöspores, a fact which confirms our previous belief that these plants belong to the present family. The narrow connection between the oögonium and the next segment below it becomes quite solid, and the apical end of the latter segment is usually somewhat swollen and gives rise to the, commonly two, antheridial branches. The oöspores, when mature, are quite thick-walled and of uniform and moderately granular appearance (Fig. 120).

The antheridial branches are composed of one or two cylindrical segments each, and are at first uniformly filled with protoplasm and applied to the oögonium (Fig. 119). Later, a part of a segment may be cut off by a transverse wall (Fig. 120), and then apparently constitutes an antheridium. The part cut off in Fig. 120 will be seen to be quite empty, and similar cases are frequent; but I have never been able to recognize fertilization tubes homologous with those of the *Saprolegniæ*. On the other hand, the whole segment may become nearly or quite emptied, as shown in the right hand branch in Fig. 121. The left hand branch in the same figure shows a condition observed in a number of instances, which is one of much interest. The limited material at hand did not permit extended observations as to its significance, but the facts appeared to be as follows in all of the several similar specimens ob-

served. In the basal part of the branch there are formed, in a single row, several globular protoplasmic masses with distinct walls. The spaces around the individual spheres seem to be separated by faint false walls of protoplasmic substance, probably formed from the protoplasm of the segment. These spheres produce structures which can be compared to nothing but germ tubes in their appearance and growth; and I have seen them in all stages from the beginning of their formation to the length shown in Fig. 121. They ordinarily grow towards the oögonium, but I have seen two of them, developed from two spheres contained in the same segment, directed away from it. In this last case they were in the lower segment of a branch of two segments whose upper member showed the same condition as that drawn in Fig. 120. While one's first inclination may be to regard these peculiar structures as specialized male cells which produce fertilization tubes of a different type from those of the *Saprolegnieæ*, yet the emptying of the apical parts of some branches, even of the same ones that contain the spheres, and the fact of the growth of their tubes away from the oögonium in one observed case, make it quite as probable that they are parasites in the antheridial branches. Yet if they are parasites, it is remarkable that they should not have been seen in other parts of the plant. I have not been able to observe what follows the contact of their tubes with the oögonium, not having seen them late enough in their history.

The general incompleteness of these observations, which bring up many interesting possibilities, can justify nothing more than the suggestion of some of these possibilities. The emptying of the separated apical parts of some branches without any evident formation of fertilization tubes needs further investigation; it is not impossible that this species may be shown to differ from the *Saprolegnieæ* which have been studied, in the occurrence of a truly sexual process. It is greatly to be hoped that some one may soon have the opportunity of studying abundant material of this plant.

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‡ As the manuscript of the present memoir was completed before the appearance of this synopsis of the family, I have not been able to refer to it.

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EXPLANATION OF PLATES.

Plate XIV.

- Fig. 1. A fly attacked by *Saprolegnia* sp. $\times 2$.
- Fig. 2. Rhizoids of *S. mixta*, giving rise to an external hypha, *h*. $\times 130$.
- Fig. 3. Cut-off ends of hyphæ of *Saprolegnia* sp. repaired by the formation of a cellulose wall. $\times 200$.
- Fig. 4. Protoplasm and nuclei of a portion of an hypha of *A. racemosa*. $\times 940$.
Picric-acid-Hæmatoxylin specimen; the protoplasm somewhat retracted from the walls by the action of the acid.
- Fig. 5. Nuclear division in an hypha of *A. apiculata*. $\times 1400$.
- The nucleus, showing chromatin-mass, nuclear membrane, and the intermediate space.
 - The chromatin-mass has elongated with the rest of the nucleus.
 - The chromatin mass is dividing.
 - The nuclear membrane is formed between the daughter-nuclei, which have not yet separated. Corrosive-sublimate-Hæmatoxylin preparation.
- Fig. 6. A bit of *L. lacteus*, showing monopodial branching and two cellulul granules, *c*. $\times 540$.
- Fig. 7. Two stages in the development of the zoöspores of *A. Americana*, showing only the base and tip of the sporangium. $\times 350$.
- The first separation fairly marked, at 11.10 A.M.
 - The "homogeneous" stage, at 11.23.
- Fig. 8. A sporangium of *Saprolegnia* sp., with zoöspores in the act of escaping, some already out, *z*. $\times 540$. Osmic-acid-anilin-violet preparation.
- Fig. 9. Four zoöspores of *A. Americana* fixed at the moment of escape; from two sporangia, *a* and *b*. $\times 540$. Osmic acid-anilin-violet preparation.
- Fig. 10. Four sporangia of *A. Americana* successively developed by cymose branching, in the order of the figures 1 to 4; the empty spore-membranes still adhering to two. $\times 200$.
- Fig. 11. The tip of a sporangium of *Aphanomyces* sp., with the head of spore-membranes, most of which have been vacated by the spores; showing a living spore, *z*, in its second form, its cilia not clearly visible, and a similar spore, *z'*, killed with iodine to show its cilia.
- a-i*, a series of stages in the development of a spore which germinated *in situ*, without the second swarming: *a*, at 10 A.M.; *b*, at 10.09; *c*, at 10.14; *d*, at 10.19; *e*, at 10.29; *f*, at 10.40; *g*, at 11; *h*, at 11.45; *i*, at 12 M. $\times 540$.
- Fig. 12. Two encysted zoöspores of *A. apiculata*. $\times 800$. Corrosive-sublimate-Hæmatoxylin preparation.
- Fig. 13. Beginning of the germination of a zoöspore of *A. racemosa*, after one division of the nucleus. $\times 940$. Picric-acid-Hæmatoxylin preparation.
- Fig. 14. Renewal of sporangia of *Saprolegnia* sp. by growth of new ones into the empty membranes of old ones. $\times 200$.
- Fig. 15. Empty, "nested," membranes of successive sporangia of *Saprolegnia* sp., the order of their development shown, 1 — 6. $\times 200$.
- Fig. 16. A part of a sporangium of *Dictyuchus* sp.; showing several stages in the escape of the zoöspores, and a mature zoöspore, *z*. $\times 540$.
- Fig. 17. Branching of hyphæ below empty sporangia in *Aph. scaber*. $\times 540$.

Plate XV.

- Fig. 18. Chlamydospores of *A. Americana*. $\times 200$.
 Fig. 19. Chlamydospores of *Achlya* sp. $\times 74$.
 Fig. 20. Germination of chlamydospores of *Achlya* sp. $\times 74$.
 Fig. 21. Origin of oögonium, *o*, and antheridium, *a*, from an hypha of *A. Anzoviniana*. $\times 200$.
 Fig. 22. A divided oögonial branch of *A. apiculata*, bearing three oögonia. $\times 200$.
 Fig. 23. A proliferous oögonium of *A. polyandra*. $\times 200$.
 Fig. 24. An oögonium of *A. Americana* which has reverted to the vegetative condition and given rise to new sexual organs. $\times 540$.
 Fig. 25. Antheridial branches of *A. Americana* terminated by oögonium like swellings. $\times 350$.
 Fig. 26. Four stages in the development of the oöospheres of *A. apiculata*; *a*, the parietal layer still intact, the protoplasm accumulating into masses, at 11.50 A.M.; *b*, the parietal layer ruptured and withdrawn into the three distinct masses, at 12 M.; *c*, the separation of small portions from the main protoplasmic masses, at 12.10 P.M.; *d*, the reabsorption of these masses, at 12.18 P.M. $\times 350$.
 Fig. 27. A still later stage than 26, *d*, the oöospheres quite rounded off, at 12.23 P.M.; showing also the antheridial branches. $\times 350$.
 Fig. 28. An oögonium of *A. papillosa* which has reverted to the vegetative condition and produced three hyphæ with sporangia, one of them fully shown at 2. $\times 200$.
 Fig. 29. Germination *in situ* of the oöspores of *A. Americana*; *a*, two spores with young germ tubes; *b*, one oöspore with a fully developed hypha and empty sporangium. $\times 540$.

Plate XVI.

- Figs. 30-36. Cytology of the sexual organs of *A. Americana*. From Corros.-subl.-Hæmatoxylin preparations.
 Fig. 30. Young oögonium with its central vacuole formed, its nuclei irregularly scattered. $\times 540$.
 Fig. 31. Oögonium after the formation of its basal wall, the protoplasm more withdrawn from the centre and the nuclei approaching in pairs. $\times 540$.
 Fig. 32. The nuclei larger, fewer, and fainter, and the vacuoles formed in the protoplasmic layer. $\times 800$.
 Fig. 33. The vacuoles have disappeared and the protoplasm is more contracted. $\times 800$.
 Fig. 34. The oöspores are formed, and the antheridia have produced fertilization-tubes which contain protoplasm and nuclei, but remain closed; *a* and *b*, two sections from the same oögonium. $\times 540$.
 Fig. 35. A fully developed oösphere with its single nucleus. $\times 800$.
 Fig. 36. Two oöospheres before the final nuclear fusions. $\times 800$.
 Figs. 37-39. *Saprolegnia monoica*.
 Fig. 37. Sexual organs, mature. $\times 540$.
 Fig. 38. Both sexual organs from the same branch. $\times 540$.
 Fig. 39. An intercalary oögonium. $\times 200$.
 Figs. 40-42. *Saprolegnia mixta*.
 Fig. 40. Two small oögonia, one with and one without an antheridium, the latter formed inside an empty sporangium. From Mississippi. $\times 200$.
 Fig. 41. An oögonium with antheridia. From Pennsylvania. $\times 200$.
 Fig. 42. An abnormally branched sporangium, not rare in this species. From Pennsylvania. $\times 74$.
 Figs. 43-45. *Saprolegnia ferax*. From Kentucky.
 Fig. 43. An oögonium, on a branch growing through a sporangium. $\times 540$.
 Fig. 44. A cylindrical oögonium. $\times 540$.
 Fig. 45. Two oögonia on a forked branch. $\times 200$.

Figs. 46-49. *Saprolegnia torulosa*.

Fig. 46. An oögonium with an antheridium, a rare case. $\times 200$.

Fig. 47. Two cylindrical members of a series, the upper an oögonium, the lower a sporangium. $\times 200$.

Fig. 48. Four members of a series, an oögonium, two sporangia, and the lowest still young. $\times 200$.

Fig. 49. Two oögonia in series. $\times 200$. The pits in the oögonial walls of this species are too inconspicuous to be brought out often with this power.

Plate XVII.

Figs. 50-53. *Saprolegnia diclina*.

Fig. 50. The mouths of two sporangia appearing as if burst open by a force from within. $\times 200$.

Fig. 51. An oögonium, with numerous antheridia. $\times 200$.

Fig. 52. A similar oögonium on a very short branch, its pits few and small. $\times 540$.

Fig. 53. An oögonium of the small form mentioned in the text. $\times 200$.

Figs. 54, 55. *Saprolegnia asterophora*. From Cambridge, Mass.

Fig. 54. A two-spored oögonium with two antheridia; after a sketch by Prof. Trelease. $\times 850$.

Fig. 55. A one-spored oögonium; from a slide by Prof. Trelease. $\times 540$.

Figs. 56-59. *Saprolegnia Treleaseana*. From Wood's Holl, Mass.

Fig. 56. The only sporangium yet seen, with a zoöspore, *z*; after a sketch by Prof. Trelease. $\times 250$.

Fig. 57. An hypha with two oögonia, one terminal, and one intercalary. $\times 74$.

Fig. 58. A terminal oögonium, without antheridia. $\times 350$.

Fig. 59. An intercalary oögonium, with antheridia. $\times 350$.

Figs. 57-59, from a slide by Prof. Trelease.

Figs. 60-68. *Pythiopsis cymosa*.

Fig. 60. Two clavate sporangia, one young, *a*, and one empty, *b*. $\times 200$.

Fig. 61. Two globular sporangia, one with its escape-papilla formed and with signs of spore-formation. $\times 200$.

Fig. 62. Four sporangia arising by cymose branching of an hypha. $\times 350$.

Fig. 63. Escape of zoöspores from a sporangium with several papillæ, only one of which has opened; *z*, three zoöspores killed soon after their escape; *z'*, two encysted zoöspores. $\times 350$.

Fig. 64. A smooth-walled oögonium with a very short antheridial branch. $\times 540$.

Fig. 65. An oögonium with two outgrowths of its wall; the antheridial branch longer than in 64. $\times 540$.

Fig. 66. An oögonium with a single large outgrowth and an antheridial branch of declinuous origin. $\times 540$.

Fig. 67. An oögonium with two ripe oöspores. $\times 540$.

Fig. 68. A ripe oöspore showing its excentric structure, with several oil globules. $\times 940$.

Plate XVIII.

Figs. 69-73. *Achlya Americana*.

Fig. 69. A recently emptied sporangium, with the spore head. $\times 200$.

Fig. 70. An hypha bearing numerous sexual organs. $\times 74$.

Fig. 71. Details of oögonial and antheridial branches. $\times 350$.

Fig. 72. A part of the ruptured wall of an oögonium, after treatment with chloroiodide of zinc, showing pits. $\times 540$.

Fig. 73. Two ripe oöspores, showing their excentric structure. $\times 540$.

Figs. 74-77. *Achlya megasperma*.

Fig. 74. Hypha bearing sporangia and oögonia. $\times 74$.

Fig. 75. The end of an hypha, with oögonial and sterile antheridial branches. $\times 74$.

Fig. 76. An oögonium with rather numerous antheridial filaments. $\times 200$.

Fig. 77. An oögonium on a longer branch, with a single antheridium. $\times 200$.

Figs. 78-81. *Achlya polyandra*.

Fig. 78. A sporangium with empty spore-membranes. $\times 200$.

Fig. 79. An oogonium on a strongly recurved branch, showing the separation of oosphere origins, with two antheridial branches. $\times 200$.

Fig. 80. A young oogonium, with much divided antheridial branches. $\times 200$.

Fig. 81. Details of oogonium and antheridia. $\times 540$.

Plate XIX.

Figs. 82-86. *Achlya apiculata*.

Fig. 82. Two sporangia. $\times 200$.

Fig. 83. A young oogonium with three antheridia. $\times 200$.

Fig. 84. An unusually recurved oogonial branch. $\times 200$.

Fig. 85. The more typical form of oogonial branch. $\times 200$.

Fig. 86. Details of a small oogonium with two antheridia. $\times 540$.

Figs. 87-89. *Achlya oblongata*.

Fig. 87. Hypha with sporangium and apical and lateral oogonia, antheridia omitted. $\times 74$.

Fig. 88. Hypha with several racemosely arranged oogonia, tending to a pointed form. From Louisiana. $\times 74$.

Fig. 89. An oogonium with several antheridial branches. $\times 200$.

Figs. 90, 91. *Achlya oblongata*, var. *globosa*. From Alabama.

Fig. 90. An oogonium showing the oöspores grouped at one side. $\times 200$.

Fig. 91. Details of sexual organs. $\times 200$.

Figs. 92-95. *Achlya racemosa*.

Fig. 92. A sporangium. $\times 200$.

Fig. 93. An oogonium with a single antheridium. $\times 200$.

Fig. 94. Details of sexual organs of the commonest form, with two antheridia. $\times 540$.

Fig. 95. Two oöspores, showing centric structure. $\times 540$.

Figs. 96-98. *Achlya racemosa*, var. *stelligera*.

Fig. 96. A young oogonium, with three antheridia. $\times 200$.

Fig. 97. An oogonium with a single very small antheridial branch. $\times 200$.

Fig. 98. Details of sexual organs. $\times 540$.

Plate XX.

Figs. 99-102. *Achlya papillosa*.

Fig. 99. An hypha with a sporangium and an oogonium. $\times 200$.

Fig. 100. A terminal and an intercalary oogonium, with antheridial branches. $\times 200$.

Fig. 101. A strongly apiculate terminal oogonium. $\times 200$.

Fig. 102. A terminal oogonium with a single antheridial branch. $\times 540$.

Figs. 103, 104. *Achlya cornuta*.

Fig. 103. Three oogonia from the same hypha, one strongly apiculate. $\times 350$.

Fig. 104. A three-spored apiculate oogonium. $\times 350$.

Figs. 105-107. *Aphanomyces lavis*.

Fig. 105. Two oogonia from one hypha, with antheridia of diclinous origin. $\times 540$.

Fig. 106. An oogonium thickly invested by antheridia. $\times 540$.

Fig. 107. A young oogonium with antheridial branches of androgynous origin. $\times 540$.

Figs. 108-111. *Aphanomyces scaber*.

Fig. 108. An oogonium of the rough form of the species, on a short, lateral branch. $\times 540$.

Fig. 109. Two oögonia on the same hypha, the lower abortive, the upper with an antheridium. $\times 540$.

Fig. 110. An oögonium of the smooth form of the species, with an antheridium. $\times 540$.

Fig. 111. An old oögonium, with a ripe oöspore and no antheridium. $\times 540$.

Figs. 112-114. *Dictyuchus Magnusii*. From Cambridge, Mass.

Fig. 112. An empty sporangium showing some of the openings for the exit of zoöspores; from a slide by Prof. Trelease. $\times 200$.

Fig. 113. An oögonium with single oöspore and antheridial branch. $\times 500$.

Fig. 114. A young oögonium with antheridial branch. $\times 500$. The last two after sketches by Prof. Trelease.

Figs. 115-118. *Leptomitius lacteus*.

Fig. 115. An empty and a young sporangium, formed from successive segments of an hypha. $\times 200$.

Fig. 116. The same, showing also the peculiar branching below a sporangium. $\times 200$.

Fig. 117. Zoöspores encysted within a sporangium. $\times 200$.

Fig. 118. Encysted and germinating zoöspores, and empty membranes pointing to diplanetism. $\times 540$.

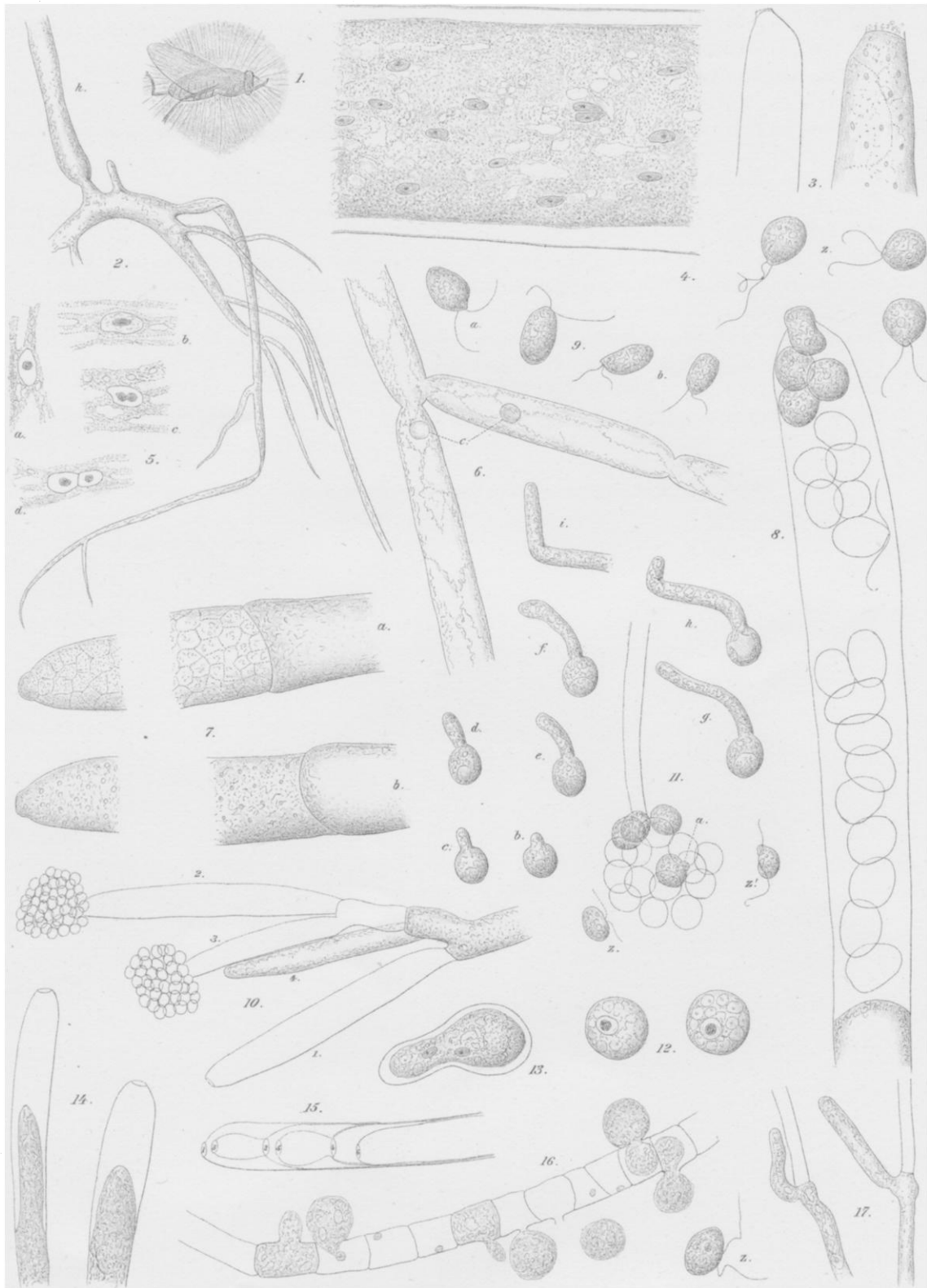
Figs. 119-121. *Apodachlya completa*. From Louisiana.

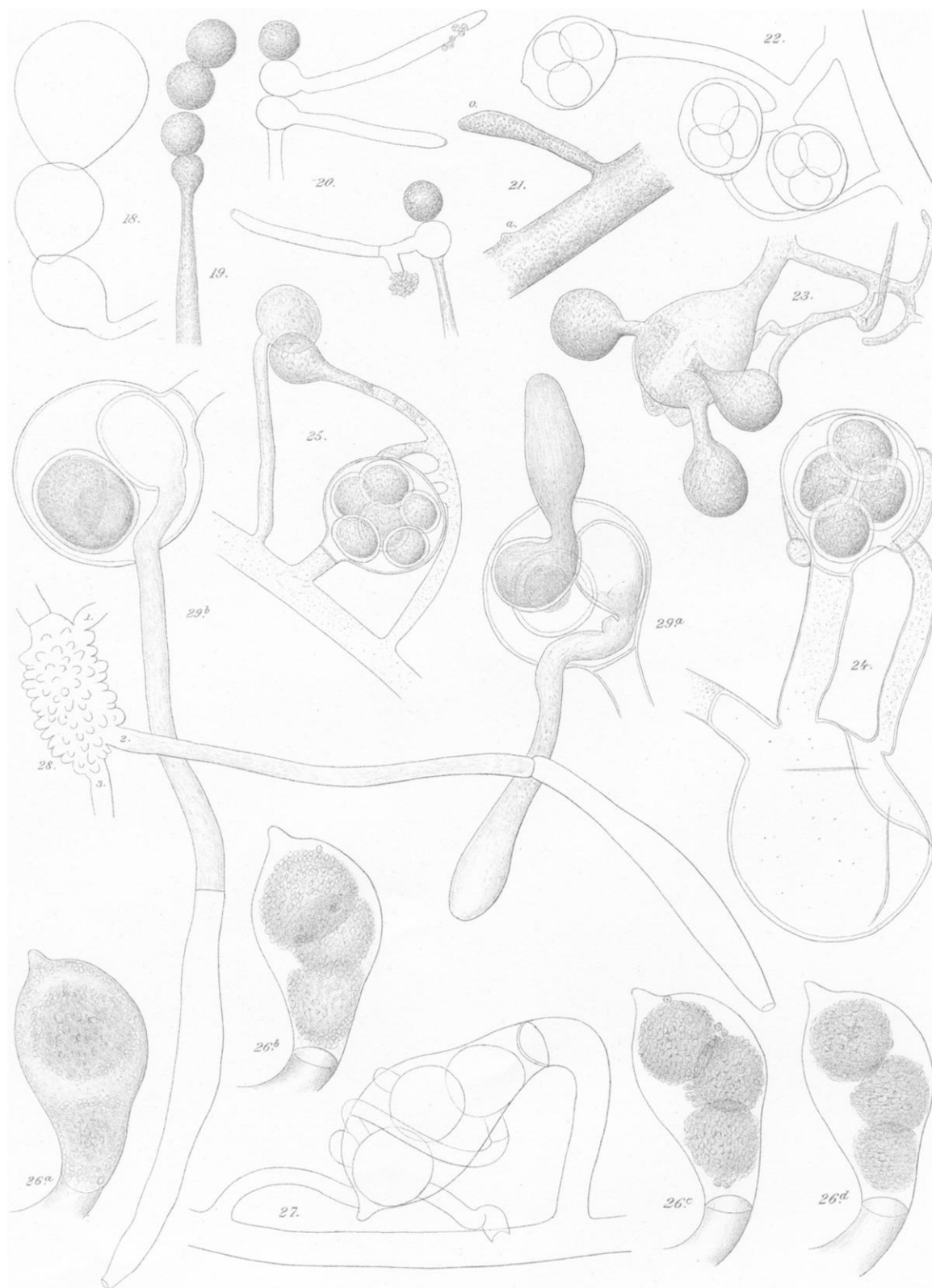
Fig. 119. Young sexual organs. $\times 540$.

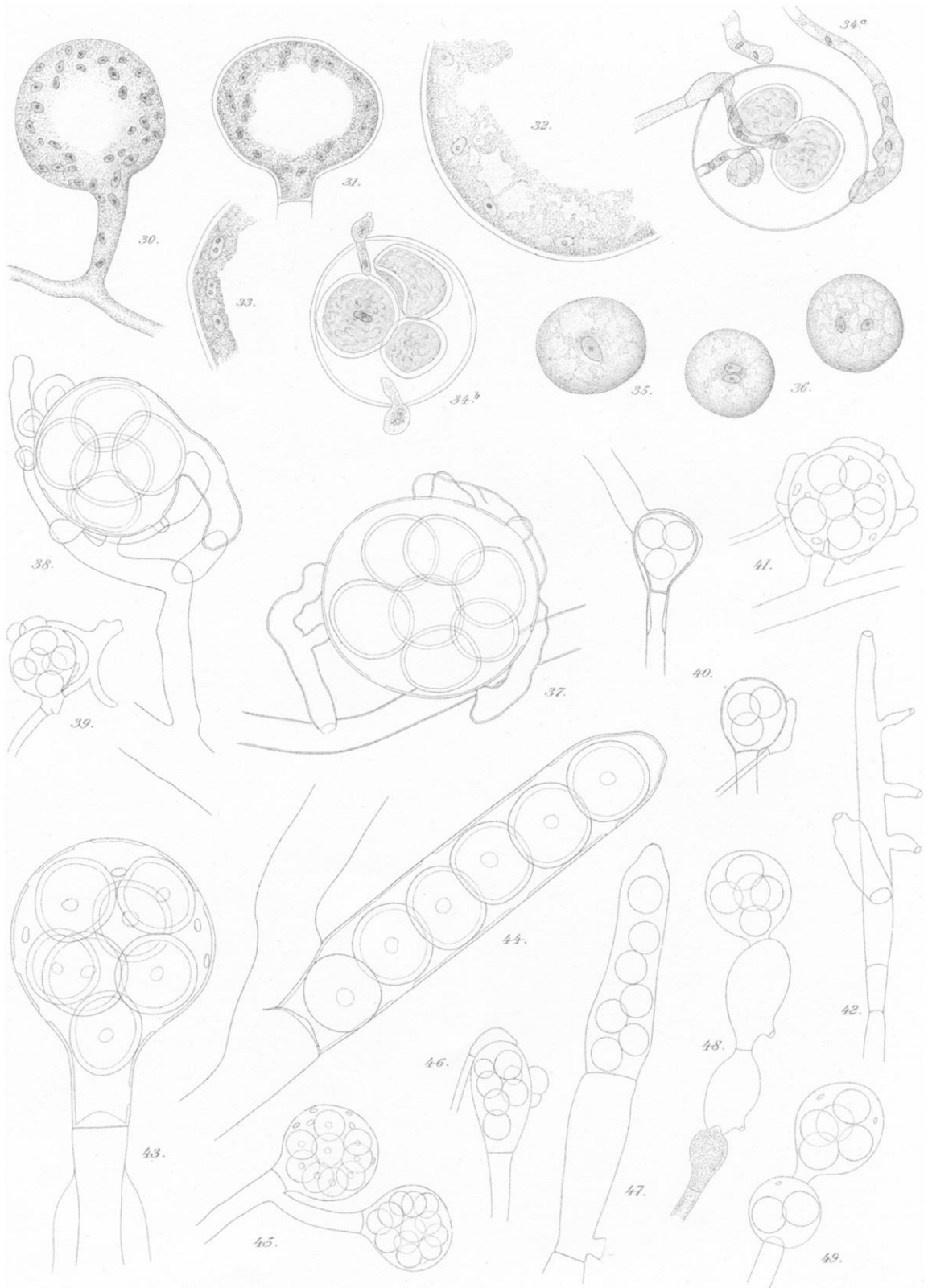
Fig. 120. Adult sexual organs, with ripe oöspores. $\times 540$.

Fig. 121. Details of sexual organs, with peculiar structure in antheridial branches. $\times 940$.

NOTE.—All drawings are from specimens obtained at Amherst, Mass., except where the contrary is noted.

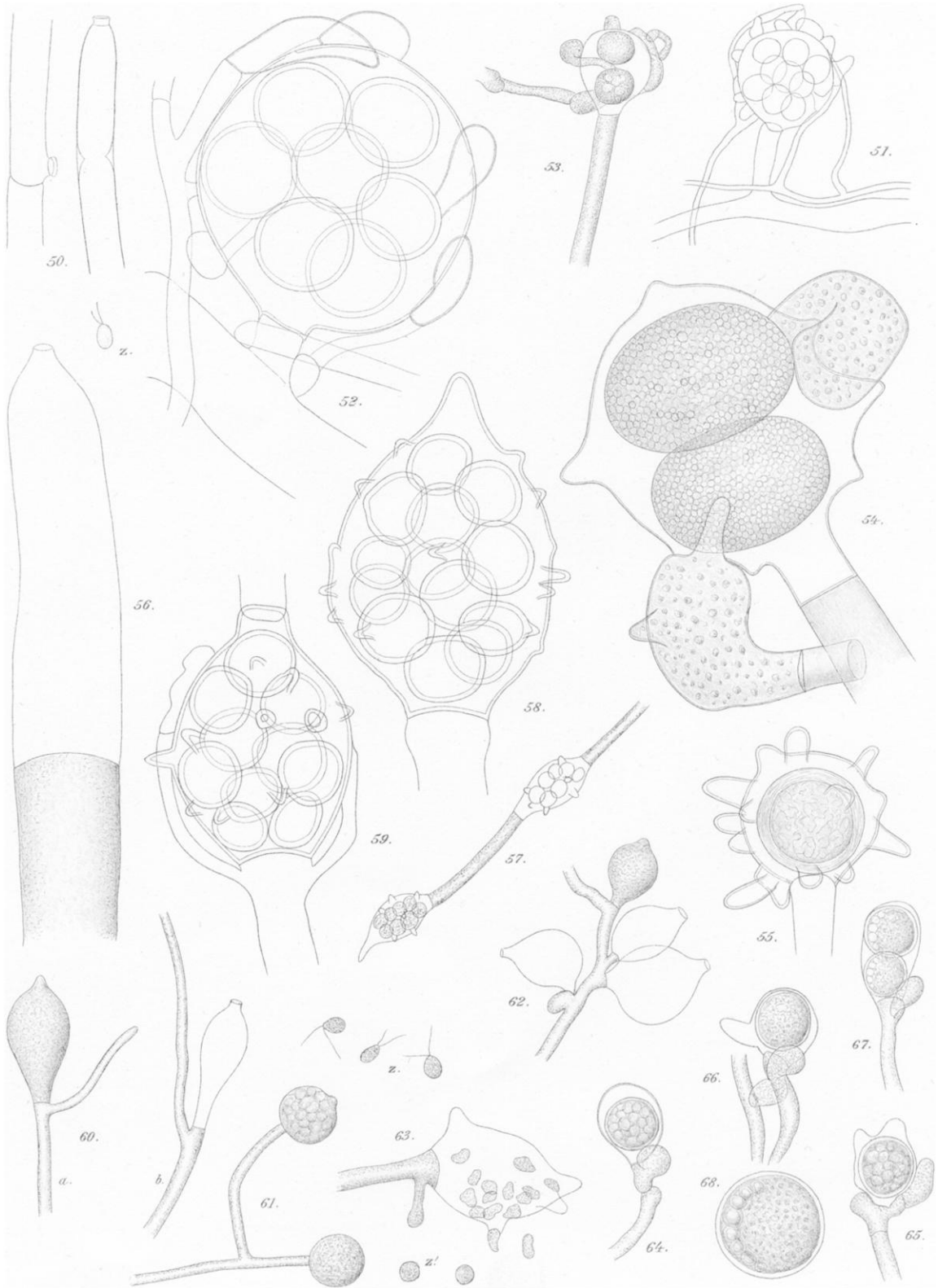


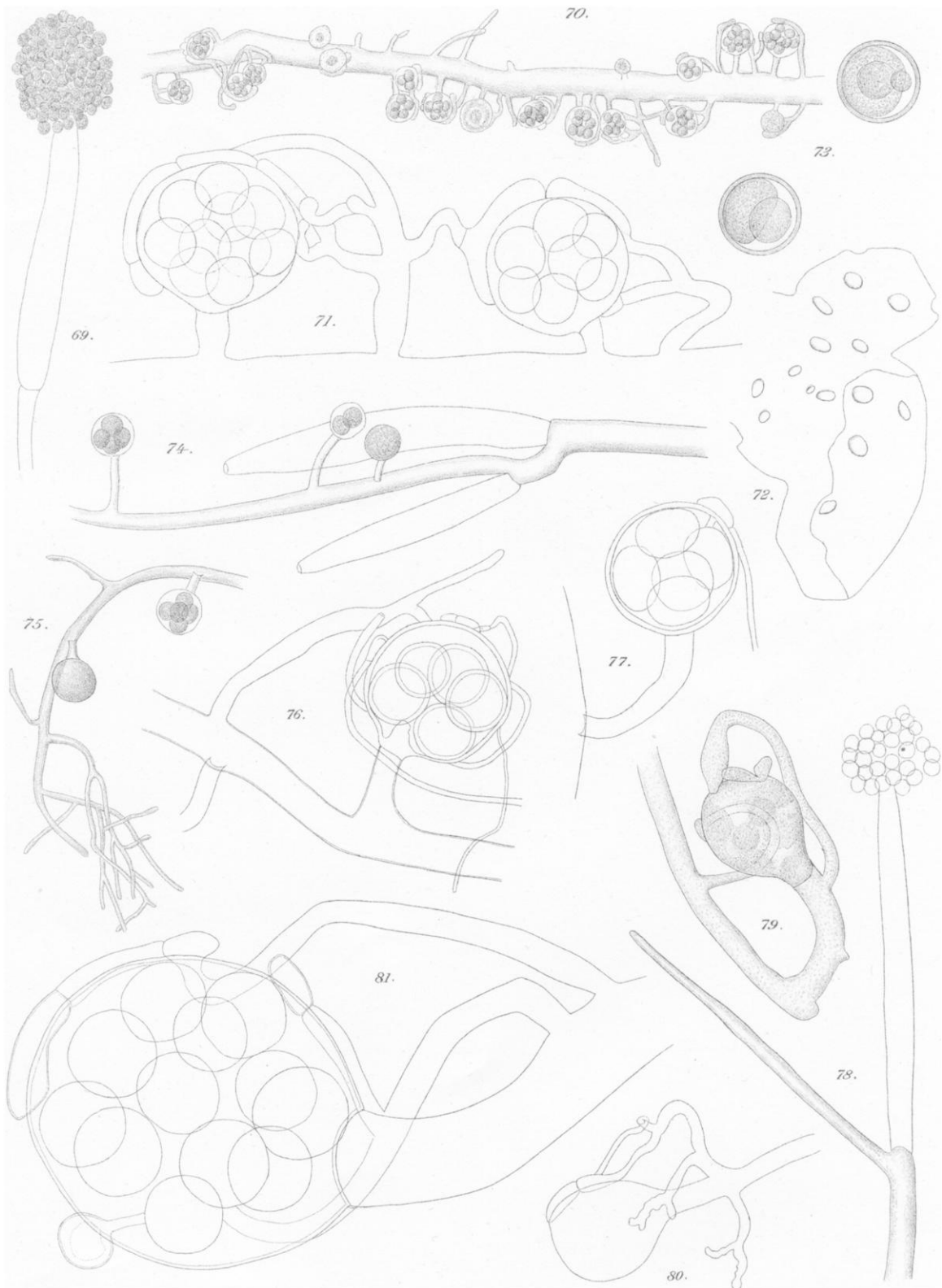




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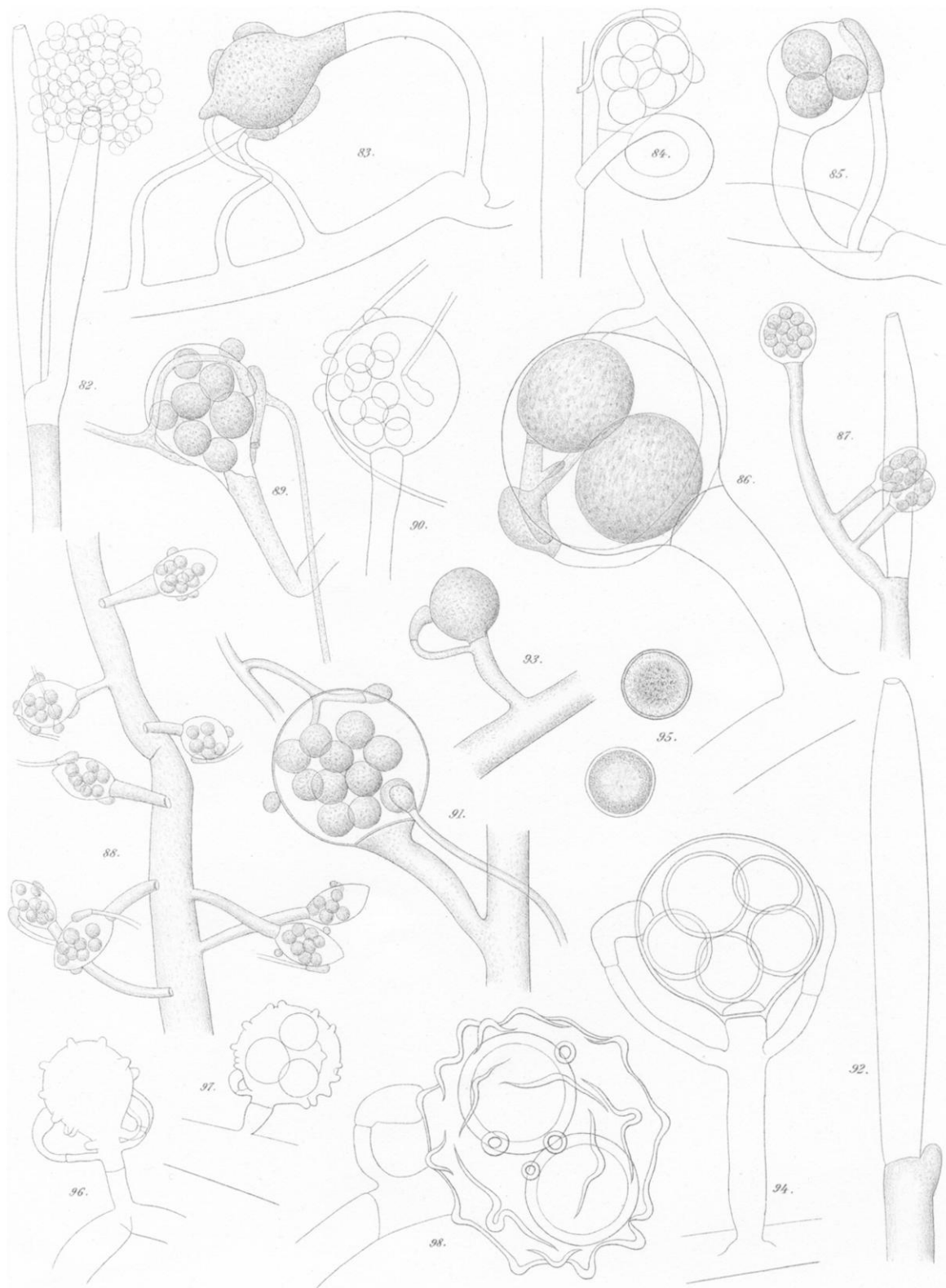
E. Meisel, lith. Boston.





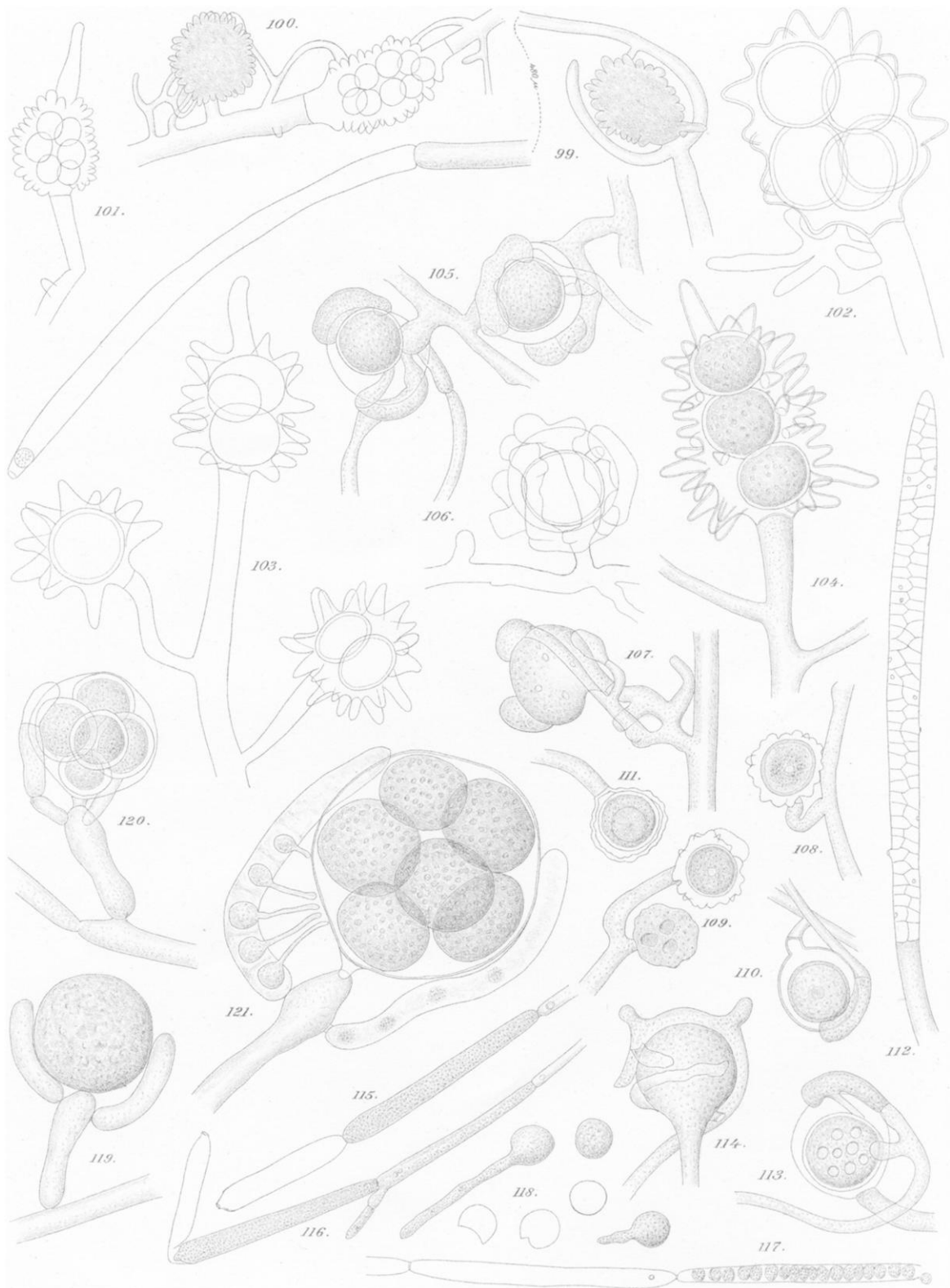
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B. Meisel, lith. Boston.



J.E. Humphrey del

B. Messel, lith Boston



J E Humphrey del

E Meisel, lith Boston

A. PAPILLOSA. CORNUTA APH. LAEVIS. SCABER. D. MAGNUSII. L. LACTEUS. APOD (?) COMPLETA.